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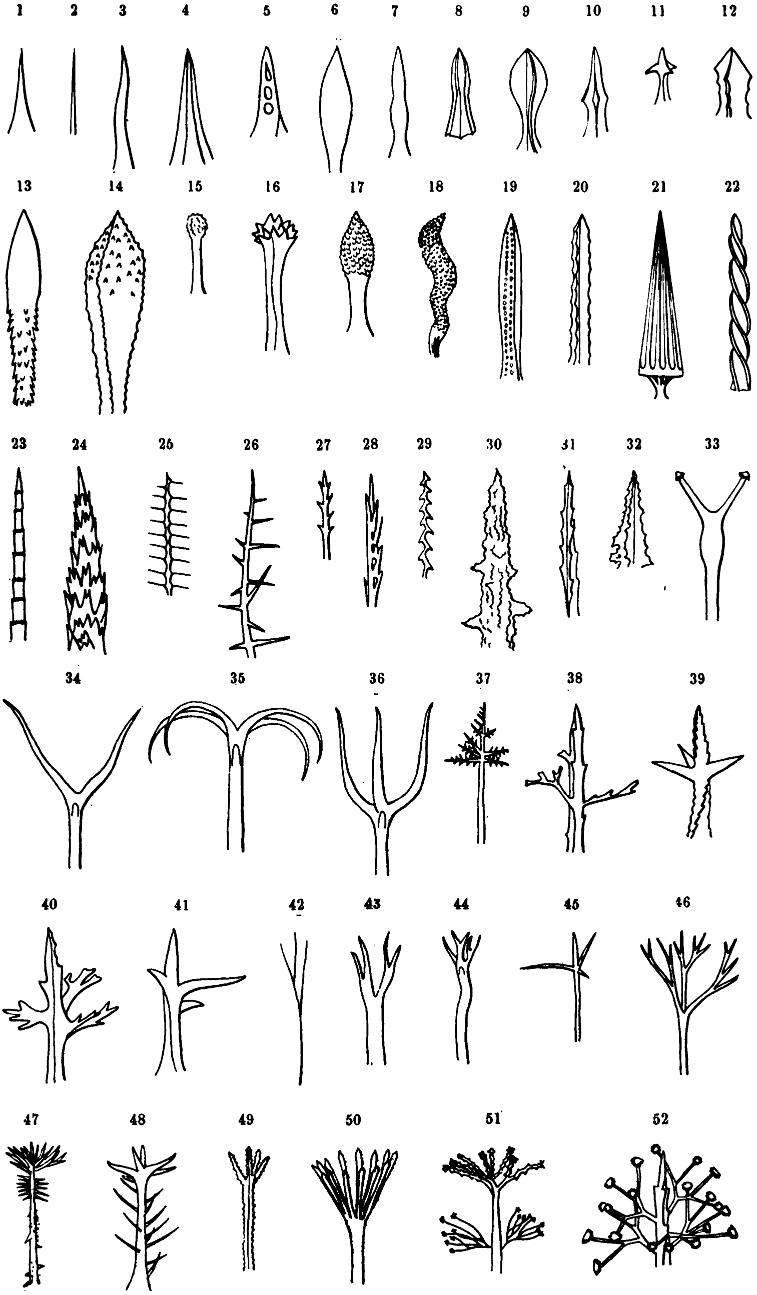
THE ORIGIN AND SIGNIFICANCE OF SPINES

A STUDY IN EVOLUTION

By CHARLES EMERSON BEECHER

Am. Jour. Sci., Vol. VI, 1898. Plate I.



SPINES OF RADIOLARIA.

THE

AMERICAN JOURNAL OF SCIENCE

[FOURTH SERIES.]

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ART. I.—*The Origin and Significance of Spines: A Study in Evolution*; by CHARLES EMERSON BEECHER. (With Plate I.)

INTRODUCTION.

THE presence of spines in various plants and animals is, at times, most obvious to all mankind, and not unnaturally they have come to be regarded almost wholly in the light of defensive and offensive weapons. Their origin, too, is commonly explained as due to the influence of natural selection, resulting in the greater protection enjoyed by spiniferous organisms. But when, upon critical examination, it is seen that some animals are provided with spines which apparently interfere with the preservation of the individual, that other animals develop spines which cannot serve any purpose for protection or otherwise, and that spines themselves are often degenerate or suppressed organs, then it becomes evident that the spinose condition may have other interpretations than the single one of protection.

The object of this article is to make a few observations on spinosity, especially among invertebrate animals, and to endeavor to arrive at some general conclusions relating to the origin and significance of this condition. It is believed that the results have a broader application than is at first apparent, and underlie important laws and principles of organic evolution. In closely related species, the presence or absence of spines seems in itself a trivial character, indicating at best only specific differences, yet it will be shown that the spines are often the expression of important vital adjustments and conditions, and are not merely external features of the same value as color and many other skin or superficial characters. As will be indicated later on, spines may also arise through the operations of a number of forces and conditions, and it may well be asked, therefore,—Do spines have any profound significance? It must be granted at the outset that apart from other characteristics, or when regarded as simple spiniform extensions of certain tissues or organs, they have no such value or meaning. How, then, should they be considered? The reply is evident: Their importance lies not in what they *are*, but in what they *represent*. They *are* simply prickles, thorns, spines, or horns; they *represent*, as will be shown, a stage of evolution, a degree of differentiation in the organism, a ratio of its adaptability to the environment, a result of selective forces, and a measure of vital power.

After studying numerous organisms, the writer is led to believe that in every case no single reason is sufficient to account for this spinose condition. The original cause may not be operative through the entire subsequent phylogeny, so that spines arising from external stimuli and then serving important defensive purposes may at a later period practically lose this function; or spines may become more and more developed simply by increasing diversity of growth forces, or through the multiplicity of effects. In this way, causes may follow, overlap, or even coincide with each other; but in interpreting special cases, the problems involved may be quite complicated and often obscure.

In reviewing the development of animal life from the earliest Cambrian to the present, one cannot avoid being impressed by the groups of spinose forms which appear here and there throughout geologic time, and give a special phase to contemporary faunas. Tracing these one by one through their geological development, it is noticed that each group began its history in small, smooth, or unornamented species. As these developed, the spinose forms became more abundant until after the culmination of the group is reached, when this type either became extinct or was continued in smaller and less specialized forms. In applying this principle to any order of plants or animals, several precautions are necessary. The estimate must be based approximately upon the general average of the totality of specific characters, whether a genus, family, order, or even a class is being considered. A short-lived family or genus, or the terminal members of specialized groups, therefore, cannot be taken as representing the developmental status of the larger divisions, because they culminated and disappeared independently of the culmination of the class to which they belong. On a small scale, however, each epitomizes the rise and decline of the larger group, and the principles of correlation commonly applied in ontogeny and phylogeny can likewise be used in the study of spines and spiniferous species, with equally exact results, whenever the principal factors are understood.

Law of Variation.

Before undertaking any general or special examination of the life histories and interpretation of spinose organisms, it is desirable to consider briefly some of the biogenetic principles which are considered to bear directly on the problems here under discussion.

First among these is the law of variation or change, which is so generally recognized as to require but the briefest restatement.

The organic as well as the inorganic world is subject to all the forces of nature, internal and external, molecular and molar, and even a partial stability is gained only through a regulated adjustment. In organisms, this change is momentary and persistent, while in most inorganic substances, it is slow and intermittent. The results of this continual readjustment constitute modification, which may be progressive or regressive, continuous or discontinuous (in the sense of accelerated, uniform, or retarded). They are everywhere present and the causes always operative. Throughout life, the individual changes, and in addition varies from all other individuals. The family, also, changes with time, and likewise differs from other families. Variation is everywhere present. Moreover, it is generally accepted, and is so taken here, that, in its results, this variation is not haphazard, but is normally in accordance with certain demands or in harmony with certain surroundings. Whether an organism itself tends to vary in all directions, or is chiefly subject to modifications from external forces, does not alter the preceding statement.

Cope[11] has considered variation as either physico-chemical (molecular) or mechanical (molar). The influence of the first is known as physiogenesis and of the second as kinetogenesis. In the animal kingdom, the potency of kinetogenesis is greater as an efficient cause of evolution; while in the vegetable kingdom, physiogenesis is apparently of more importance.

The tendency of variation is always in the direction of the establishment of an equilibrium between the organism and its environment. However, the laws of the development of the earth preclude the possibility of a constant environment, and therefore a perfect, permanent, and uniform equilibrium between life and surroundings is unattainable.

The manner of variation is clearly defined as *progressive* and *regressive.* Progressive variation is one of the essential factors of evolution, while regressive variation is towards dissolution. Since the main history of life is told through processes of the former, progressive variation is far greater in importance; while, in general, regressive variation can be applied only to late periods in the history of groups or forms now in their decadence, or to others which in past times have suffered decline and extinction.

The summary of the operation of the law of multiplication of effects, as given by Herbert Spencer[66], may well be stated here, as it emphasizes one of the principles through which spines have originated.

"It manifestly follows that a uniform force, falling on a uniform aggregate, must undergo dispersion; that falling on an aggregate made up of unlike parts, it must undergo dispersion from each part, as well as qualitative differentiations; that in proportion as the parts are unlike, these qualitative differentiations must be marked; that in proportion to the number of the parts, they must be numerous; that the secondary forces so produced must undergo further transformations while working equivalent transformations in the parts that change them; and similarly with the forces they generate. Thus the conclusions that a part-cause of evolution is the multiplication of effects, and that this increases in geometrical progression as the heterogeneity becomes greater, are not only to be established inductively, but are deducible from the deepest of all truths."

Modification, therefore, may properly include the results of the multiplication of effects. Furthermore, from a knowledge of the life history of the organic world, it is known that this change has been progressive, resulting in the evolution of the higher from the lower, of the complex from the simple, and of the definite from the indefinite.

It must now be asked,—Is the amount of variation without limit or is it restricted within bounds which can be determined? As far as can be seen, the limitations of the forms of species of animals and plants end only with the aggregate number of possibilities within the functional scope of the organism. Beyond, in either direction, is death, and a passage from the organic into the inorganic. The restrictions of variation are chiefly those of temperature, pressure, motion, light, space, time, and matter. Within certain limits, these clearly bound the horizon of known possible life. Further, the material constitution of the organic world is naturally subject to ordinary mechanical and chemical laws.

If, instead of the preceding, general, and therefore rather abstract statements of the limits of variation, the subject is considered from the concrete, objective side, the limits between which are found all the variations actually presented by any character or set of characters, in the animal or the vegetable kingdoms, can at once be determined. The fact that the organic world can be divided into kingdoms, sub-kingdoms, classes, orders, etc., and definitions of the divisions given, in itself furnishes sufficient evidence that these have been the limits of organic change, at least under present terrestrial conditions. This does not imply that the phylogenies of groups of animals and plants do not converge and coalesce, and join larger and larger phyla in past ages, so that the gaps between unlike forms are gradually filled by complete series. It does, however, express the definite heterogeneity of the results of development.

For the sake of illustrating an extreme range of variation, it will be granted that the assemblage of characters by which a mammal is now recognized precludes mammalian variation into a cold-blooded, non-vertebrate, lungless animal. Likewise, the mammalian skeleton cannot be siliceous or chitinous. Externally, mammals may be smooth, hairy, scaly, or plated, but not feathered. There may be found numerous gradations from the smooth to the plated state, and a great range of variation in each type of epidermal structure. In vertebrate animals generally, the hair may vary in length, in fineness, in color and shape; it may form bristles, or spines, or feathers; and as a skin character, it is related to horn-sheaths, hoofs, nails, claws, scales, and teeth. These constitute the limits of modification in epidermal or exoskeletal growths. The types are few, but the variety in each is almost infinite. The variation may be seen in individuals, but becomes greater in species, and increases still more in larger groups. The gradations are numerous between the hair of a Beaver and the spines of a Porcupine; between the horns of the Giraffe, Rhinoceros, and Antelope; between the nails of Man and the claws of the Carnivora; and between the teeth of a Dog-fish and those of a Tiger.

Definition of Terms.

In the beginning, it is well to understand the meaning and extent of the terms included under the comprehensive word spine. In a general sense, *spine* is here used to cover any stiff, sharp-pointed process. A *prickle* is restricted in use to the small, sharp-pointed, conical projections which are purely cuticular; as in the Rose and Blackberry. A *thorn* is a sharp process on plants, usually representing a branch or stem. A *horn* is an excrescence on the head of certain animals, and is properly hollow. An *antler* is a solid bony process, usually deciduous, and generally confined to the male; as in the Deer or Elk. A *spur* is a term applied to the claw-like process on the legs and wings of some birds, and on the hind legs of *Ornithorhynchus* and *Echidna.*

The word spine, therefore, is most comprehensive, and is here intended to include the modified hairs of the *Echidna* and Porcupine; the sharp, prickly scales of the Horned Toad (*Phrynosoma*); the pointed spiniform projections on the shells of Mollusca; the spinous prominences on the test of Crustacea and insects; the fin spines as well as those on the opercula and scales of fishes; the generally movable processes of Echinoderms; the projecting rays and processes of Radiolaria, etc., etc. The vertebral column and also the processes from the separate vertebræ are known as spines, but as these are distinctly internal structures, they will not be considered in this connection.

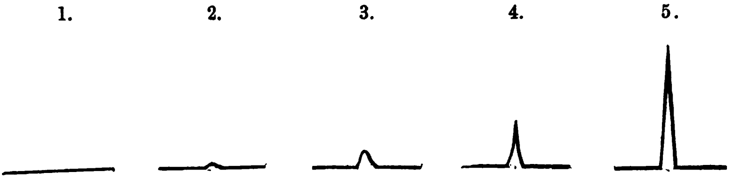
In nearly all classes of organisms, spines have been developed independently, and simply represent cases of parallel development of similar structures or morphological equivalents. They possess analogy of form without necessary homology of structure, and accordingly have no common phylogenetic connection. Therefore, if the relationships between the smooth and spinose forms belonging to any group of animals or plants can be traced, and the simplest and most primitive condition in each case, as well as the highest stage of progressive development, can be ascertained, their relative significance from an evolutionary standpoint may be confidently determined.

Growth of a Spine.

The growth of a spine is either direct and progressive, or indirect and regressive. It is direct when it is developed by the addition of new tissue. In this way, growth is attained in the antlers of a Deer, the horns of a Cow, the ordinary spines of Brachiopods, Mollusca, and Crustacea, and in other similar examples covering the majority of cases. Growth is indirect, however, when the spine represents atrophy or suppression of an organ through the loss of its accessory parts, as in the thorns of the Locust and the Barberry, the spiniform termination of the stems of the Pear, or the spurs on the Python.

The direct development of a spine is essentially the same process in all cases. At a given point on the surface of an organism, there first appears a slight elevation, which becomes higher and higher, and is usually conical in form. This cone represents the simplest type of spine; and among animals and plants, most spines conform to this primitive pattern (figures 1–5).

Often there are various kinds of surface ornaments, which by growth and differentiation develop into spines. By rhythmic, alternating areas of accelerated or retarded growth, the concentric laminæ on many molluscs may produce spines, as shown in figure 26. In the same way, the radiating ridges may be diversified into a row of spines, as represented in figure 6. Further, the surface may be reticulate, with longitudinal and transverse lines, and at the points of intersection, nodes and often spines are formed after the manner shown in figures 7–12. The longitudinal or vertical lines may become obsolete, leaving the spines to be borne on the transverse or horizontal lines (figure 10). In other cases, the horizontal lines disappear, leaving the spines on the vertical lines (figure 11). Finally, both horizontal and vertical lines become obsolete, and then only the spines remain, as shown in figure 12.



FIGURES 1–5.—Different stages in the growth of a spine. 1, plane surface; 2, slight elevation; 3, node; 4, short spine; 5, completed simple spine.

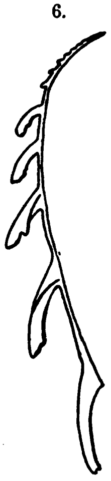
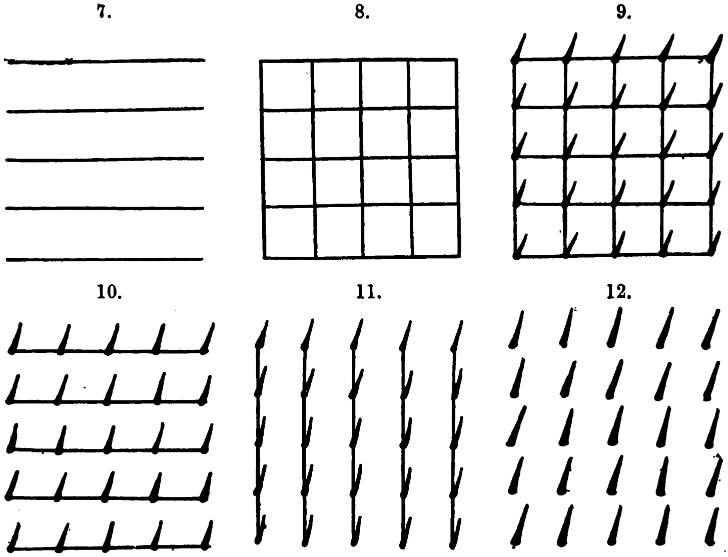


FIG. 6.—A profile of a single radiating ridge of *Spondylus princeps*, showing the series of flattened spines.

The indirect production of spines is not always evident, for if the ontogeny or phylogeny of the individual is unknown, its direct or indirect development cannot be determined. An excellent example of indirect, or regressive, growth of spines is afforded in the common Barberry (*Berberis vulgaris*), on the summer shoots of which are shown most of the gradations "between the ordinary leaves, with sharp bristly teeth, and leaves which are reduced to a branching spine or thorn. The fact that the spines of the Barberry produce a leaf-bud in their axil also proves them to be leaves"[24] (figure 13).

It should be noted that the process of spine development illustrated in *Spondylus* (figure 14) is directly opposed to that of the Barberry. In the former, the initial growth is smooth, then faint concentric and radiating lines appear, which gradually grow stronger, developing more or less regular inequalities; and by the excessive growth of these variations, spines are formed. In the Barberry, there are at first normal leaves, which are followed by others more and more toothed and bristly, until the leaf is represented by a branching spine, while finally spines only are formed. The *Spondylus* represents a progressive increase in growth to produce the spines, while the Barberry exhibits a progressive decrease of growth, or an "ebbing vitality," as it has been termed by Geddes.[20]



FIGURES 7–12.—Diagrams showing growth and differentiation of ornament into spines. 7, surface with parallel lines; 8, surface with regular reticulate lines; 9, same, with spines developed at the points of intersection; 10, same, with the vertical lines obsolete, but still represented by the vertical rows of spines; 11, same, with the horizontal lines obsolete, but still represented by the horizontal arrangement of the spines; 12, same, with all lines obsolete, but both series represented by the vertical and horizontal arrangement of the spines.

The spines are the final results of both the direct and indirect modes of production; the direct, through a process of building on new tissue, and the indirect, through a process of dwindling away to all but the axial elements. These differences are graphically expressed in figures 13 and 14.

Attention should be called to the four kinds of spine production in different organisms. (1) In the Radiolaria, Echinoids, the Giraffe, Cattle, and the Rhinoceros, the spines or horns are persistent, and grow by additions to the original structure. The new tissue may be superficial, subterficial, interstitial, or formed by synchronous resorption and growth. (2) In the Crustacea and Articulata generally, and in the Deer, Elk, etc., the spines are moulted, or shed, periodically. In their various stages, these types (1 and 2) can be studied only by means of separate specimens consecutive in age, or by observing the metamorphoses in one individual. (3) In the shells of Brachiopods and Mollusca, the stages of growth of the individual are generally retained throughout life, and the

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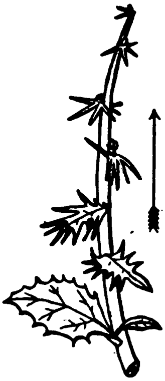

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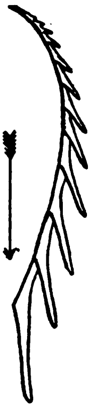

FIGURE 13.—Summer shoot of Barberry, showing the gradations between leaves and spines. The arrow indicates the direction of growth. (After Gray.)

FIGURE 14.—Profile of one of the primary rays of *Spondylus imperialis*, showing the series of spines. The arrow indicates the direction of growth.

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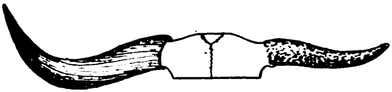

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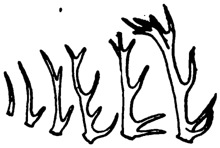

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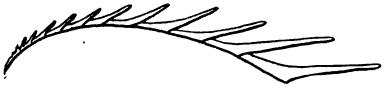

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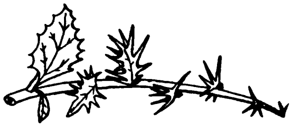

FIGURE 15.—Example of spine growth by simple increscence. Horn (left) and horn-core (right) of Ox. (After Owen.)

FIGURE 16.—Stages of spine growth by successive replacement. Antler series of Red Deer, at ages of 1, 2, 3, etc., years. (After Owen.)

FIGURE 17.—Stages of spine growth by serial repetition. Profile of a series of spines on one of the primary radii of *Spondylus imperialis*.

FIGURE 18.—Stages of spine growth by decrescence. Transformation of leaves into spines in *Berberis vulgaris*. (After Gray.)

successive development of spines may be studied, therefore, in a single example. (4) Spines produced by suppression, as in the Barberry, express their origin through a series of gradations between separate parts; while in others, suppression is brought about by the loss of structures.

The first type mentioned develops horns or spines by simple increscence (figure 15); for example, the Ox: the second, by successive replacement (figure 16); as in the Deer: the third, by serial repetition (figure 17); for example, *Spondylus:* the fourth, by decrescence (figure 18); for example, the Barberry.

Localized stages of growth.—By the multiplication of surface ornaments through the process of interpolation, many Mollusca present stages of spine development in two directions. (1) The normal series is represented by the succession of spines along a

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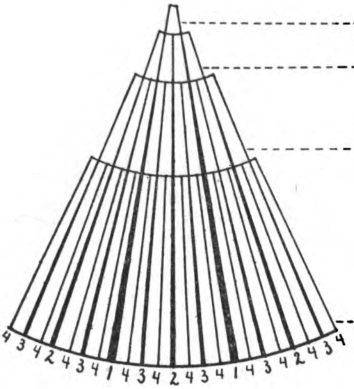

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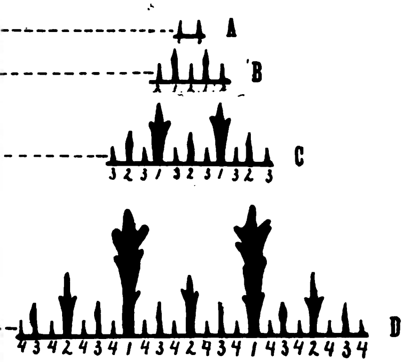

FIGURE 19.—Sector showing in diagram the multiplication of radiating lines by interpolation. The two primary radii (1, 1) are the only ones continuing through the whole four zones. The first zone has 2 radii; the second, 5; the third, 11; and the fourth, 23.

FIGURE 20.—Profiles of the spines produced on the various radii at the four zones, as indicated in the preceding figure. A, the spines on the two primary radii of the first zone; B, the spines on the second zone, showing the growth of those on the two primary radii (1, 1), and the small spines on the newly interpolated radii (2, 2, etc.); C, the spines on the radii in the third zone; D, the spines at the bottom of the fourth zone. The two large compound spines are on the two primary radii. Their development may be traced by following them through A, B, C, to D. The next three longest spines (2, 2, 2) are tricuspid, and represent the stage of spine development attained by the spines on the radii which were interpolated on the second zone. The next six smaller spines (3, 3, 3, etc.) are on radii which were introduced on the third zone. The twelve small spines (4, 4, 4, etc.) are on the radii introduced on the fourth zone. Thus there are four stages of spine growth shown on the lower margin of the fourth zone, and these correspond to the four stages exhibited by the series of spines on one of the primary radii running through the four zones.

single sector of growth. For instance, in the radial plications of a *Spondylus* or *Lima*, the earliest and primitive spines are found near the beak, while those on the ventral border of an adult specimen are the latest and most highly developed (figure 30). These successive stages, therefore, are in the direction of growth, and may be called longitudinal. (2) By the radial divergence of the ribs or plications and the interpolation of additional ones at various intervals, as many transverse compound series of spines finally appear along the periphery as there are primary radii. Hence, in a given case, there may be two radii continuing to the beak, then by interpolation there are successively 5, 11, 23, etc., radii, the highest number being found at the periphery (figures 19, 20). Moreover, by taking the distal spines on these 23 rows, there result the same stages of spine development as shown in the longitudinal series along any primitive plication (figure 20). A Pelecypod shell like *Spondylus* is here used to illustrate this process, but the application may also be made to the Brachiopods as well as to the conical non-coiled Gastropods. In a coiled form like a Cephalopod or an ordinary Gastropod, the longitudinal lines would follow the whorls spirally, and the transverse lines would correspond to the lines or increments of growth of the shell. Species in which the radii are all introduced at an early stage of growth (many species of *Cardium*, *Pecten*, *Lima*) or in which the radii multiply by regular dichotomy would show, of course, only the longitudinal series, for at the margin of the shell, the radii would be of the same size and age, and the spines uniform.

The foregoing example illustrates an important principle of ontogeny; namely, that in organisms which repeat various parts during their growth, these parts will develop or pass through a series of stages corresponding to the initial and subsequent stages of the parts repeated. In this way, structures appearing late in the ontogeny of the individual will present primitive infantile and adolescent characters. Further development, if such takes place, will pass through a progressive series of ontogenetic changes, and if the stages of growth are by serial repetition and thus are retained in the part, it will be found that such stages can be correlated with those appearing early in the life or history of the individual. Therefore, in studies of this kind, it is possible to take a structure appearing at maturity, and from it deduce or predicate as to what were some of the early characteristics of the whole individual. This principle is termed localized stages of growth by Jackson[37], and was first noticed by him in some investigations on Echinoderms.

Compound Spines.

A simple, sharp, conical process expresses only the primitive type of spine. In plants and animals, it is the most common form found, and is the first stage of spine differentiation. From this type, the myriad forms of spines known in the organic world are produced by almost insensible gradations. It is needless to attempt a detailed description of this infinite variety; but, as a single illustration, some of the leading forms of spine differentiation among the Radiolaria are here shown (Plate I). These figures are taken from Haeckel's "Report on the Radiolaria,"[26] and generally represent enlargements of from 100 to 400 diameters.* Probably no other class of

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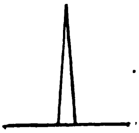

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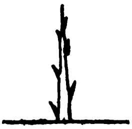

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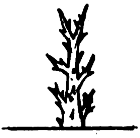

FIGURE 21.—Simple spine.
FIGURE 22.—Spine, with lateral spinules.
FIGURE 23.—Spine, with forked apex and lateral spinulose spinules.

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* EXPLANATION OF PLATE I.

Spiniform processes of recent Radiolaria taken from the shells of the following species:

Fig. 1.—Heliosphæra coronata.
Fig. 2.—Astrosphæra stellata.
Fig. 3.—Astrophacus solaris.
Fig. 4.—Stylosphæra calliope.
Fig. 5.—Heliodiscus glyphodon.
Fig. 6.—Pripodictya triacantha.
Fig. 7.—Pleuraspis horrida.
Fig. 8.—Hexacontium sceptrum
Fig. 9.—Acanthosphæra clavata.
Fig. 10.—Acanthosphæra clavata.
Fig. 11.—Cromyodrymus quadricuspis.
Fig. 12.—Hexacontium clavigerum.
Fig. 13.—Orosphæra horrida.
Fig. 14.—Staurocyclia phacostaurus.
Fig. 15.—Tripospyris capitata.
Fig. 16.—Archipera cortiniscus.
Fig. 17.—Tripospyris conifera.
Fig. 18.—Orosphæra serpentina.
Fig. 19.—Staurolonche pertusa.
Fig. 20.—Astrosphæra stellata.
Fig. 21.—Staurodictya elegans.
Fig. 22.—Hexastylus contortus.
Fig. 23.—Stephanospyris excellens.
Fig. 24.—Podocyrtis magnifica.
Fig. 25.—Hexancistra mirabilis.
Fig. 26.—Dictyophimus Cienkowskii.
Fig. 27.—Elatomma juniperinum.
Fig. 28.—Castanura tizardi.
Fig. 29.—Pleuraspis horrida.
Fig. 30.—Staurocarynum arborescens.
Fig. 31.—Rhizosphæra serrata.
Fig. 32.—Phænocalpis petalospyris.
Fig. 33 —Aulospathis bifurca.
Fig. 34.—Aulographis bovicornis.
Fig. 35.—Aulographis ancorata.
Fig. 36.—Aulographis bovicornis.
Fig. 37.—Sphærozoum verticillatum.
Fig. 38.—Cladococcus pinetum.
Fig. 39.—Hexancistra triserrata.
Fig. 40.—Cladococcus stalactites.
Fig. 41.—Hexancistra quadricuspis.
Fig. 42.—Heliodrymus ramosus.
Fig. 43.—Heliodrymus dendrocyclus.
Fig. 44.—Aulographis pandora.
Fig. 45.—Cladoscenium ancoratum.
Fig. 46.—Cladococcus scoparius.
Fig. 47.—Auloscena penicillus.
Fig. 48.—Circostephanus coronarius.
Fig. 49.—Lychnosphæra regina.
Fig. 50.—Auloscena spectabilis.
Fig. 51.—Cœlospathis ancorata.
Fig. 52.—Octodendron spathillatum.

organisms presents greater variety, and many of the forms are repeated again and again, not only in various species of this group, but elsewhere both in the animal and vegetable kingdoms.

Whenever the development of a compound spine can be studied, it shows a gradual progress from the simple to the complex (figures 21–23). The antlers of the Red Deer (*Cervus elaphus*) furnish a familiar example. Fawns of the first year have antlers with only a single prong, a short front tine being added the second year; then "year by year as they are renewed they acquire a greater and still greater number of tines and branches, till they finally attain the complete stage, when their owner is termed a 'royal hart'"[44] (figure 16). Although somewhat conventionalized, the primary series of spines on the *Spondylus* shown in figure 20 exhibits the passage from simple to compound forms. An inspection of many species of *Murex* will show the stages in series presenting a greater complexity.

After spine development has reached its maximum growth and differentiation, evidence of old age may be exhibited in two ways: (*a*) The spines may be reduced by resorption, decay, or abrasion, and finally become obsolescent; or what is of greater import (*b*), they may gradually cease to be developed, as is especially shown in organisms in which spine growth is by serial repetition. Thus, in *Spondylus calcifer*, a young individual measuring about two inches across has marginal spines fully an inch in length. Even longer spines are found when the shell reaches a width of four inches. On attaining a maximum diameter of about six inches, spine growth gradually ceases, and the margin of the valves is entire and nearly smooth. At this stage, shell secretion is confined to excessive thickening of the valves. These senile stages of spine growth will receive further consideration under the discussion of ontogeny and phylogeny of spinous species.

Application of law of morphogenesis.—The manner in which spines arise from plane surfaces, or from the growth or modification of superficial structures, and also through the decadence of organs, has now been noticed. The spine may thus be taken as a unit for comparison, and its various stages of growth, which were shown to have a definite sequence, may be used in correlation to determine relatively the degree of spine specialization attained by any organism. Furthermore, enough data have been already given to lead to the suspicion that spines may represent the limits of ornamental or superficial differentiation or variation. At this point in the discussion, this statement must be considered as more suggestive than conclusive. The proof of its reality will be more clearly shown later on.

Ontogeny of a Spinose Individual.

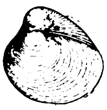
With few exceptions, the embryonic and larval stages of all organisms are devoid of specialized surface features. In other words, they are without ornament and without weapons. The exceptions to this rule seem to be readily explained under the principles of larval adaptations and accelerated development. Cases of the latter kind, therefore, can hardly be considered as exceptions, since they represent, not real larval features, but former adult characters which have been pushed back or which develop earlier so as to appear eventually in the larval or later embryonic stages. In the very earliest stages of embryonic development, the truth of the first statement becomes obvious, and accordingly the protembryonic, mesembryonic, metembryonic, neoembryonic, and typembryonic stages are without surface ornaments or spines.

Among Mollusca, the protoconch, periconch, and prodissoconch, or the early larval shells, are smooth and without ornament. Even the prodissoconch of very highly spinose species, as in *Spondylus*, is as smooth as that of the plainest species of *Ostrea*, *Anomia*, *Avicula*, etc. Likewise, the protoconch of the most specialized or most retrograde Cephalopod is perfectly plain. In the nepionic stages, the spiny *Murex* is without spines. In the Brachiopoda, the protegulum, or early larval shell, is always without sculpture; while the nauplius of Crustacea and the protaspis of Trilobites are generally spineless. The young of horned vertebrates are almost universally hornless, the Giraffe being the only mammal born with horns. The very young seedlings of plants are likewise spineless. In insects, the embryonic stages generally have simple cuticles, but in the larval stages of this class and the Crustacea, a great variety of spines and ornamental characters is developed. Altogether, it may be asserted that spines do not appear during the embryonic stages of animals and plants, and that their initial development is commonly post-larval.

Examples illustrating the ontogeny of a spinose form could be multiplied indefinitely, and taken from nearly every class of organisms. In all cases, practically the same sequence of events relating to the development of spines would be found. The organism would first be smooth, without sculpture or ornament, like the young of other organisms. At some stage of the ontogeny, the beginnings of spines would appear, and develop first into simple, and later, according to the stage of differentiation attained, into compound spines. This progression would finally reach the maximum, spine growth would cease, and the surface of the organism would inversely revert to an early and more primitive type without spines. Normally, these changes would represent the infantile, adolescent, mature, and early and late senile periods of the life of the organism. In some cases, however, the stages of spine growth, or acanthogeny, do not agree with the ontogeny of the entire individual in respect to time, and here acceleration and the phylogeny of the species will be found to offer the proper explanation of the divergence.

As simple examples of the ontogeny of spiniferous species, the Mollusca afford especial advantages, owing to the fact already noticed, that the stages of development are commonly preserved in a single individual. In figure 24, the larval shell, or prodissoconch, of Pelecypods, or bivalve shells, is represented, and shows the usual type throughout a large portion of the class. The succeeding shell growth of the dissoconch is at first generally smooth, save for the fine concentric lines of growth (figure 25). In ornamented or spinose species, however, irregularities in the growth lines soon appear (figures 26, 27), and these shortly assume the characteristic surface sculpture of the normal adult. Thus, the prodissoconch of *Avicula sterna* is represented at *p*, figure 25, and is followed by regular concentric growth during the nepionic stages. In figure 26,

24.



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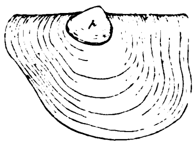

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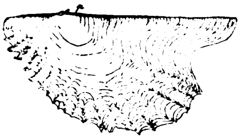

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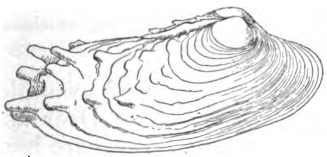

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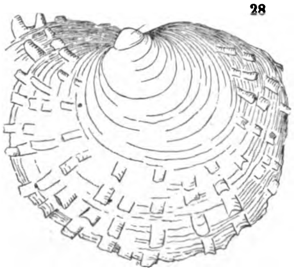


FIGURE 24.—Prodissoconch of *Ostrea virginiana*. × 43.

FIGURE 25.—Each stage of *Avicula sterna* ; *p*, prodissoconch. × 19.

FIGURE 26.—Young *Avicula sterna*, showing the beginning of spine growth. × 3.

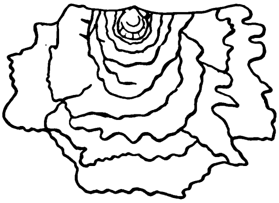
FIGURE 27.—Young *Saxicava arctica*. × 19.

FIGURE 28.—Young *Anomia aculeata* ; *p*, prodissoconch succeeded by early smooth and later spinous dissoconch growth. × 30. (24–28 after Jackson.)

the spiny characters of early adolescence are added to the previous stages, and in later stages, the spines become more and more emphatic.

In *Spondylus*, the prodissoconch is the same simple form, and is succeeded by a nearly smooth Pecten-like stage, during which the animal was free (figure 29). After fixation, the growth is very irregular and ostræiform for a time, until the shell rises above the object of support, when all the most characteristic features of surface ornamentation become fully developed (figure 30). As the shells approach maximum growth, the spines gradually become shorter, and in old age, none are developed, even those of early growth being removed by the action of boring animals and by solution (figure 31).

29.



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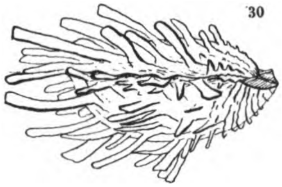

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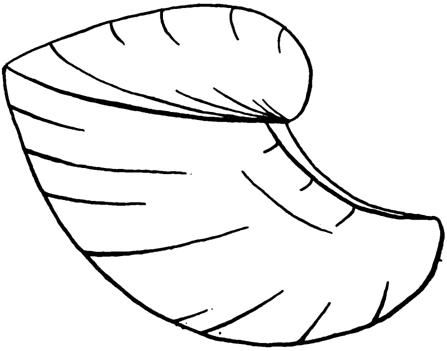

FIGURE 29.—Young *Spondylus princeps.* Right valve, showing pecteniform stage succeeded by ostræiform growth. Taken from apex of adult specimen; presented by R. T. Jackson. × 3.

FIGURE 30.—Side view of *Spondylus calcifer*, about one-third grown, showing the characteristic spinous growth. ½.

FIGURE 31.—Side view of *Spondylus calcifer*, showing the greatly thickened right valve and the entire absence of spines over the whole shell. ¼.

It seems unnecessary to increase the number of examples showing the ontogeny of spinose individuals. The Deer and the Ox may be again cited in this connection. Both are born without horns, but during adolescence, the antlers of the Deer become longer and more complicated with each renewal, while the horns of the Ox are longer and more twisted. In old age, when the Deer has passed his prime, the antlers are more obtuse, and exhibit a tendency toward decline and obliteration. Suppression of the antlers is accomplished by the removal of the cause of antler growth and specialization, so that the unsexing of the male results in small antlers, which are seldom branched, and become thickened by irregular deposits of bone (Owen[53]). Spines grow during the adolescence of the Horse-Shoe Crab, *Limulus polyphemus*, yet in old age they are obsolescent, being represented by rounded nodes.

As examples illustrating the accelerated development of spines in widely separated classes, the Giraffe among mammals and *Acidaspis* among Arthropods may be selected. The Giraffe represents the continuance of a very primitive type of horn; namely, one covered with a hairy skin. They are never shed, and are common to both sexes. Out of this type, all others found among the Mammalia have probably been developed. The point of interest here is that the young Giraffe is born with horns, and as these could serve no prenatal purpose, it must be concluded that the action of accelerated heredity has pushed the development of these organs so far forward as to cause them to appear during fœtal growth.

The next illustration of acceleration is taken from the Trilobites. *Acidaspis* is one of the most highly specialized and ornate genera. Although the larval forms of other genera are commonly without ornament, yet in the present genus, the protaspis, or phylembryonic, stage partakes of this specialization in so far as to develop minute spines, which later become larger, more differentiated, and form a conspicuous feature of the adult. Other characters have been likewise shown to appear at an earlier period than in other genera, and the earlier inheritance of spines must be explained in the same manner.[8]

The facts, as stated, seem to warrant the conclusion, that in spinose organisms, the very young are almost universally without spines. Acceleration may occasionally push their development into the embryonic and larval stages, but ordinarily they are not so subject to the action of this law as are some of the physiological and other structural characters. This will be explained as in part due to the lack of general plasticity, and because differentiated spine growth is the progressive limit of variation. Therefore, there are no subsequent characters to displace them and crowd them forward in the ontogeny.

Phylogeny of Spinous Forms.

To interpret phylogeny in terms of ontogeny, according to the law of morphogenesis, or recapitulation, is perhaps easier than to trace a genetic sequence through a series of forms having a considerable geologic range. Taking the ontogenies of the animals already noticed, there is for the Pelecypods the prodissoconch, which is correlated by Jackson[36] with *Nucula*, and a Lower Silurian nuculoid radicle is assumed for the

Aviculidæ and allied forms. The first dissoconch growth produces a shell resembling *Rhombopteria*, a Lower and Upper Silurian type, and this is taken to represent the second stage in the phylogeny of *Avicula* (figure 25), *Anomia*, *Spondylus*, etc. Continuing the development of *Spondylus*, it is found by Jackson that it passes successively through stages which may be correlated with *Pterinopecten* (Devonian), *Aviculopecten* (Devonian), *Pecten* (Carboniferous ?), and *Hinnites* (Trias), while finally it assumes true spondyliform characters. These correlations agree with the geologic sequence of the genera, and are believed to indicate phylogenetic relationships. It may be further remarked that the early species of Spondyli are more truly pecteniform and hinnitiform than the later ones. The genus ranges from the Trias to the present. Zittel[78] remarks that "the oldest species are small, thin-shelled, and seldom much ornamented." Even in the Cretaceous, the majority of species are not far removed from *Pecten* and *Hinnites*. During the Tertiary, the irregular, ostræiform, squamous, concentric, and spinous growth becomes more manifest, and at present most of the species show a great development and differentiation of the spines.

Thus, while *Spondylus* is normally considered as a spinose genus and the species are familiarly known as Spiny Oysters, yet as it is traced back in geological history, the forms become less and less spinose, and their affinities and appearances are more and more in accord with non-spinose genera, until finally the prototype is a smooth, simple, delicate, unornamented shell.

The simple antlers of the young Deer and Elk correspond in type with those of the adults of the Middle Tertiary Deer (Lydekker[44]), and it may be therefore assumed that the great number of branches and tines is a modern development. Further back in the Tertiary, the ancestors of the Deer were without antlers, thus representing in phylogeny the new-born Deer of the living type. These correlations are made from comparisons of chronogenesis, or development in time, and ontogenesis, or development in the individual.

An example of a different kind will now be given to show more clearly a genetic sequence in forms. Among the Brachiopods, *Atrypa hystrix* represents one of the terminal members or species of a line of varietal and specific differentiation, extending through the Silurian and Devonian. The type commonly known as *Atrypa reticularis* appears to have had its inception during the Ordovician; yet in the Silurian, it is found as a conspicuous and fully developed form. Here, also, it has quite a wide range of variation, but there seems to be an insensible gradation between the extremes, which, therefore, cannot be considered as definite permanent varieties. There are, however, associated forms that have received distinctive specific names, which do not shade into each other. During the early and middle Devonian, certain of these variations in the main stock of *A. reticularis* became more fixed, and at the time of the Hamilton sediments in New York, there are two forms known as *A. reticularis* and *A. aspera*, which apparently do not pass into each other. As time went on, these two types became more specialized and the divergence correspondingly increased, until in the Upper Devonian, in the Chemung sediments, there is a large many-plicated *A. reticularis*, as well as a form with very few plications and long marginal spines, *A. hystrix*. Hall and Clarke[31] thus summarize the stages leading to the formation of the spinose forms: "In the variant of *Atrypa reticularis*, occurring in the Niagara fauna at Waldron, Indiana, the free concentric lamellæ frequently show a tendency to fold inward at the summit of the principal plications. The infolded edges fail to unite, and this tendency to the formation of tubules is apparently carried no further at this period. More extreme results were attained by the *Atrypa aspera* of the Hamilton shales, or possibly by its migrated ancestor, during the period of time represented by the deposition of the Lower Helderberg, Oriskany, and Upper Helderberg sediments. At all events, the *Atrypa spinosa* of the Hamilton shales is but an *A. aspera* with the lamellæ enfolded into tubular spines. Intermediate stages connecting these different phases are not present in this fauna." . . . . "This spinose form is continued into the Chemung faunas (*A. hystrix*), with some modification of expression, the spines being few and long, and the plication of the surface very coarse and quite simple; the shell in its decline thus representing a decided return to the primitive type of structure." H. S. Williams[72] has classified the variations in the stock of *A. reticularis* as to whether differentiation in the number of plications is increased or retarded, and concludes that the extremes are most strongly expressed at the close of the life-period of the race. The numerously plicated type represents the accelerated phase of the multiplication of radii, while *A. hystrix*, with its few and coarse radii, represents the retardation or suppression of this tendency.

The only great group of animals receiving its name from its characteristically spinose surface is the Echinodermata, or the spiny-skinned animals; yet it is extremely doubtful whether this name would have been used had the first studies of the group been based upon the Paleozoic representatives, especially the pre-Devonian species. The early Sea-lilies (Crinoidea), Cystideans (Cystoidea), Blastoids (Blastoidea), and Star-fishes (Asteroidea) had smooth or nearly smooth integuments. In its early genera, even the most typically spiny class of the whole sub-kingdom, the Echinoidea (Sea-urchins) had very minute and insignificant spines. It is only in the late Devonian and in the Carboniferous that truly spiny forms of Crinoids, Star-fishes, and Sea-urchins are found.

Of equal significance is the fact that the Echinodermata together with the plants represent the most primitive type of structure, one in which there is a more or less circular arrangement of the parts or organs. The Echinodermata are the highest development in this line of growth among animals. They culminated in past geological ages, and from them no direct line of descent can be traced (Bailey[2] and Cope[11]).

The conclusion from the study of the phylogenies of spinose forms is parallel to the one drawn from the ontogenies; namely, that the ancestors of spinose as well as non-spinose organisms were simple and inornate.

[To be continued.]

ART. XII.—*The Origin and Significance of Spines: A Study in Evolution;* by CHARLES EMERSON BEECHER.

[Continued from page 20.]

CATEGORIES OF ORIGIN.

As previously shown, spines are formed either by growth or by suppression, and therefore the processes determining their production are either constructive through concrescence or destructive through decrescence. Each of these is in turn determined by forces from without the organism (extrinsic) or by forces from within (intrinsic). In this connection, it is of no especial moment whether or not the intrinsic forces are primary or are an immediate or subsequent reflex from the extrinsic. The main thing is the direction of the dominant force, whether centripetal or centrifugal. If, in some cases, it can be shown that spine development has been accomplished by intrinsic forces in the organism, then this development may be brought about independently of the environment and possibly at variance with it. Also, if in other cases, the extrinsic forces or the influences of the environment have caused spine growth, it may in some instances illustrate the formation and transmission of an acquired character, or at least the operation of organic selection.

The point has now been reached where it is impracticable to make a rigid classification of the direct factors or an exact determination of primary and secondary causes. It was remarked at the beginning of this paper, that single causes were not sufficient in every case to account for spine growth, and while it is comparatively easy to formulate abstract expressions or terms covering all possible cases, it will be found difficult to construe properly certain factors to fit into any particular conception. In illustration of this, the foregoing statements may be taken. Thus, spines are formed by the only means possible, either by growth of new tissue or by decrease in old. Again, the forces must act from the interior or from the exterior; in other words, they must be intrinsic or extrinsic. But in some specific instance, while considering food, forces of nutrition, external or internal demands, reactions, etc., a question may arise as to the proper disposition to make of a spine developing primarily by external stimuli and becoming a defense and secondarily a weapon; yet which by differentiation in time loses some of its protective and offensive qualities, and by selection may be confined to one sex.

Growth and decline are underlain by the processes taking place in individual cells as well as in aggregates of cells, for spine growth must be considered in unicellular as well as multicellular organisms.

Ryder[61] has very philosophically discussed the correlations of volumes and surfaces of organisms, and has reached the conclusion that "the physiological function of a cell is also a function of its figure, i. e., of its morphological character; that is to say, cells tend to elongate in the direction of the exercise of their function." Out of this may be deduced the correlative conclusion that aggregates of cells having a like function also tend to elongate in the direction of the exercise of this function; and, further, it may be asserted that parts or portions of cells will act in the same manner.

A familiar illustration of these principles as applied to a single cell may be taken from the Rhizopod, *Amœba proteus.* When disturbed by incident forces in all directions, it assumes a globular form. Under continuous motion of its own, it is elongated in the axis of motion, its larger pseudopodia being thrust out in more or less the same direction. The presence of a favorable exciting cause, like a particle of food, produces extension of the protoplasm to envelop it.

Furthermore, as is well known, continuous extra-pressure on any part of an organism produces atrophy and absorption, and intermittent or occasional pressure causes hypertrophy and growth. That the pressure should be intermittent, seems a necessary condition for hypertrophy, in order that the parts affected may have normal intervals allowing the active exercise of nutrition.[65] This may be regarded as a parallel statement of the law of disuse and use; the former causing organs or parts to dwindle away and lose their function, and the latter producing increased nutrition and growth.

This ratio of exchange between nutrition and waste is on the side of full or excessive cell-nutrition, producing growth in the parts affected, while deficiency of nutrition produces decline or suppression. If the successive increment constituting growth is along definite progressive lines towards higher structures, and the decrement affects the decline of useless parts or permits of the replacement of a lower by a higher structure, then the sum of the changes is progressive evolution.*

Growth, as stated, seems to require normal intervals for the proper exercise of nutrition, which involves an intermittence of the exciting or stimulating forces. Rhythm has been shown by Spencer[66] to be a necessary characteristic of all motion, and therefore in considering either the intrinsic or extrinsic forces acting on the structures of an organism, they must be rhythmic or intermittent. In the environment, the most apparent changes are those of light and darkness, heat and cold, moisture and dryness, and variations in amount of oxygen, all of which affect an organism directly, and also through the accompanying variations in the character and amount of the food supply, the number of enemies, etc. These and most of the mechanical forces of the environment are therefore intermittent, and their resultant must have a definite tendency, so that the effects are not with each change successively positive and negative to the same degree; that is, the same structures or adjustments are not alternately made and unmade.

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* This is very near Cope's idea of progressive evolution.

It is generally recognized that there is a necessity for a force or energy in living organisms, which is not the immediate and direct result of external agencies, but upon which these fall and produce reactions. It is considered as a phase or kind of vital force directing growth, and therefore a growth force, or the bathmic force of Cope.[10] The internal energy of growth, involving the capacity or effort of responding to external stimuli, is termed entergogenic energy by Hyatt.[34] Without this power, an organism would be unable to move or respond to external stimuli. The effect of the action of this kind of energy must be the resultant between "the structures already existent in the organism and the external forces themselves."[34] Since the growth force is within the organism, or inborn, it is one of the principal characters transmitted through heredity, and if it is in excess of the external forces, the modifications will be principally congenital or phylogenic. If, on the other hand, the external forces predominate, the modifications will be principally adaptive, or ontogenic. In each case, the resultant is the actual visible effect of the two. If both are toward the establishment of similar structures, their effect will be the sum of the two; but if they are opposed to each other, the effect will be their resultant, the nature of which, as seen above, will depend upon their relative power.

These conclusions can be correlated directly with the developmental variations occurring in the life history of any great group of organisms. Anyone who has studied the chronological development or the phylogeny of a class of forms cannot fail to have been impressed with the fact, that all types of life are physiologically more plastic or subject to greater changes near their point of origin. That is, the maximum of generic, family, and ordinal differentiation is found at an early period, while the greatest specific differentiation occurs at a later period. This shows that the results of variation at first affect the physiological and internal structures, and that later the changes are mainly physical and peripheral.

One explanation of this would be that the forces of the environment are at first freely transmitted and produce internal modifications, and that later these characters become stable, making the effects of the external stimuli apparent in the superficial differentiation of the organisms.

In any event, the modifications in function and structure are followed by modifications in surface, showing that the more important physiological and structural variations are the first to be subjected to heredity and natural selection, which tend to fix or hold them in check. Features of less functional importance, as peripheral characters, are the last to be controlled, and therefore present the greatest diversity, while in this diversity spinosity is the limit of progress. In order to be hereditable, the modifications through the environment must have induced correlative internal adjustments and changed forces which can be transmitted to offspring, and they in turn reproduce the specific modifications.

For the purpose of illustrating these statements, the evolution of the Brachiopods and Trilobites will be taken. The Brachiopods are divided into four orders, all of which appear in the Lower Cambrian and continue to the present time. Schuchert[61] states that "of the 49 families and subfamilies constituting the class, 43 became differentiated in the Paleozoic, and of these 30 disappeared with it"; also, "of the 327 genera now in use, 227 had their origin in Paleozoic seas, or nearly 70 per cent of the entire class." Throughout the Cambrian, "differentiation was mainly of family importance." "Differentiation is most rapid near the base of the older systems, and diminishes the force from the older to the younger geologic divisions." The most rapid increase was in the Ordovician, the culmination was in the Devonian, and the rapid decline came with the Carboniferous. About six thousand species are known, and of these probably not more than one hundred and fifty are living.

Similar data are derived from the Trilobites. This group is found all through the Paleozoic, at the close of which it became extinct. Two of the three orders are found in the Lower Cambrian. The remaining order appeared just after the close of the Cambrian in the early Ordovician, yet through the whole of the remaining sediments not a single new ordinal type was enveloped. When applied to a single order, the same truth comes out. The order Proparia is one whose entire history can be traced, extending from the Ordovician through the Silurian and Devonian. All the families appear in the Ordovician; in fact not a single family type in this or the other orders was produced during the whole Silurian, Devonian, and Carboniferous.[6]

As the classes, orders, and families are based upon the physiological and important functional structural characters or differences, it is evident that at or near the beginnings of their life history is found the demonstration of the domination of phylogenic over ontogenic characters.

Conditions or forces affecting growth.—Since spines are purely organic structures, their production must follow the general laws of organic change. The forces considered as of most consequence are two: (1) the external stimuli from the environment, and (2) the energy of growth force. These, with their opposites (1*a*) the restraint of the environment, and (2*a*) the deficiency of growth force, are believed to include the chief active and passive causes, not only of spine production, but of growth and decline in general. Correlating these four causes with their constructive and destructive agencies, together with their extrinsic and intrinsic modes of action, as previously explained, there result (A) the external stimuli of the environment as an extrinsic cause of concrescence; (B) energy of growth force as an intrinsic cause of concrescence; (C) external restraint as an extrinsic cause of decrescence; and (D) deficiency of energy of growth force as an intrinsic cause of decrescence. The remaining vital forces (nerve force, or neurism, and thought force, or phrenism) are not primary, and, although doubtless affecting growth in higher organisms, cannot be original causes applicable to all forms of life, both plant and animal.

In tabular form, the divisions and relationships of the factors of spine genesis may be expressed as follows:

Spines originate by	Constructive agencies (concrescence) acting	extrinsically (centripetally)	A from external stimuli
		intrinsically (centrifugally)	B from growth force
	destructive agencies (decrescence) acting	extrinsically (centripetally)	C from external restraint
		intrinsically (centrifugally)	D from deficiency of growth force

Under the last four divisions (A—D), it is proposed to discuss the origin of spines, and from the observations made, to derive certain conclusions regarding the significance of the spinose condition.

A. *External Stimuli.*

Under external stimuli are included all the forces of the environment (chemical, physical, organic, and inorganic) which, through their impact or influence on an organism, produce a consonant favorable change or disturbance. In general, it will be seen that the number of impressions and their power will depend largely upon the position and character of the surface upon which they impinge. The more exposed the position, the greater will be their strength and number, and if these stimuli or impressions are intermittent, and not so violent as to produce waste and rupture, growth will ensue. Under ordinary conditions, exposed parts will naturally be the first to receive sufficient stimulus to produce growth, and there will be normally a direct correlation between growth and stimulus. In a simple diagrammatic form, this would be expressed by a series of lines, the first representing a plane surface. Then, owing to the impossibility of maintaining a uniformly intermittent stimulus or a uniform response, some point or spot on this surface would grow in excess of the others. This difference would be augmented by the more favorable position of the spot to receive stimuli, further growth would take place, the growth force decreasing with the increase of distance, and the final action of these forces, stimulus and growth, would be to produce a pointed elevation. Such structures or outgrowths, especially when made of hard rigid tissue, would be termed spines under the general definition. The spine may be viewed as an attached organism, and its conical habit of growth would then conform to the law of radial symmetry, as determined by the physiological reaction from equal radial exposure to the environment. That all the irregularities of contour in all organisms have not developed into pointed processes or spines is not, therefore, the fault of the simple reciprocity between growth and external stimuli. This kind of development, however, requires a direct and immediate responsive external growth to the exciting force, which from various causes is frequently absent. Obviously, stimuli which result simply in motion or equivalent internal adjustments can have no effect toward spine production, so that only the results of such stimuli as bring about some accompaniment of superficial growth will be considered.

With the exception of perfectly spherical, freely moving forms, all organisms have certain parts which are more exposed to the forces of the environment than others, and from the principles already enunciated, such exposed parts under normal conditions will grow. This growth in the direction of function and stimulus, when acted upon by the hereditary functional and structural requirements of the organism, serves to produce the various external organs and appendages. But when the surface upon which the stimuli fall is not thus predetermined by heredity to grow into a certain organ or functional part, there results a normal responsive action between growth and stimulus, which, as already seen, tends to produce a conical or spiniform growth.

Under ordinary favorable conditions, simple external stimuli acting blindly through no agencies of selection would develop spines on all the most exposed parts, and tend to differentiate ornamental features. This has been the case with many organisms and colonial aggregates possessing no power of selection or not acted upon by any forces of determination, conscious or unconscious. In such cases, spines may or may not serve for protection, and their function, if any, can be only determined separately for each case. If, however, the added function of offense is included, it is manifest that the spines must be located in special positions adapted to use for offensive purposes as on the tails of some animals and not necessarily over vulnerable parts. Here the selective agency of special adaptation is shown. Again, if while there is agreement in other essential characters, spines or horns are confined to either sex, it is evidently a case of sexual selection. Further, if they develop in harmony with the environment, or in a manner parallel to similar features of other organisms, it is through the operation of physical selection.

Altogether, under the general forces of external stimuli, there are five aspects in which to consider the production and growth of spines, viz:

A. *From External Stimuli.*

A1.—In response to stimuli from the environment acting on the most exposed parts.

A2.—As extreme results of progressive differentiation of ornaments.

A3.—Secondarily as a means of defense and offense.

A4.—Secondarily from sexual selection.

A5.—Secondarily from mimetic influences.

B. *Growth Force.*

In unicellular organisms, growth force, or bathmetic energy, must reside wholly in the germ cell, and therefore is concerned with reproduction as well as with cell differentiation. In multicellular organisms, the growth force is in both germ and soma cells, and its relative strength seems to depend upon its power to reproduce lost parts, often including germ cells as well as soma cells. In many of the lower classes, the growth force is able to complete a structure or lost part without the stimulus of use, which in higher animals often seems to be part of the necessary requirements for growth.

Growth itself is the repetition of cells under nutrition and stimulus, and the latter may be hereditary or extra-individual. It is now recognized that since the division of a cell makes two unlike cells, each unlike the parent, such repetition will produce structures which present some degree of difference. The variation is therefore a necessary quality of growth, and its degree will change in response to the differentiation of the forces affecting growth.

When spines which have arisen from intrinsic growth force only are sought, it is apparent that they cannot be distinguished from those arising from external stimuli acting on and directing the growth force, unless, in some instances, they are found to be developed independently or even at variance with the environment. Because spines are sometimes useful to the organism, it is impossible to believe that they have originated from that cause, since their existence in some form must precede the capacity of making them useful. After they began to develop by either intrinsic or extrinsic forces, their being found useful would simply tend to their conservation and further development.

Variation which is not restricted by natural selection or a long line of hereditary tendencies is known as free variation. It is best exhibited in a stock which occupies for a considerable time a region favorable in respect to food, climate, and absence of dominating natural enemies. This relation has been called the period of "Zoic maxima" by Gratacap,[21] and has been further discussed by the same author, under the aspect of numerical intensity.[22] The most rapid rise of a stock is considered to be consequent to a favorable environment and high vitality.

In illustration of these points, the Achatinellæ of the Sandwich Islands afford a good example. The great number of species on these islands has probably been evolved since Tertiary times, and the process of specific delimitation is apparently still going on, for species are now to be found which did not exist fifty years ago (Verrill); also, a few species formerly common are now obsolescent or extinct. According to Hyatt, they all can be deducible from a single species which has differentiated in time through divergence, dispersion, and colonial isolation. In early times, birds may have fed upon them, but the complete or partial extinction of the former by man has resulted in complete immunity for the arboreal Achatinellæ, and it is now common to find several of the most highly colored varieties feeding together on the same leaf. The modern importation of pigs, sheep, and mice on the islands has introduced an enemy to the terrestrial species, the effects of which are already being noticed. In specific differentiation and in individual variation, both Hyatt and Verrill regard the extraordinary development of this type as characteristic of free variation, under favorable conditions, in a plastic stock which has not yet reached its limits nor become fixed.

Among the Crustacea, the remarkable evolution of the genus *Gammarus* in Lake Baikal,[17] and of *Allorchestes* in Lake Titicaca,[19] seem to furnish parallel examples. *Allorchestes* ranges from Maine to Oregon and southward, through the United States, Mexico, and South America to the Straits of Magellan. Before Lake Titicaca was explored, but one or two authentic freshwater species were known from both continents; yet from this lake basin alone, Faxon[19] has described seven distinct species, constituting the entire Crustacean fauna with the exception of a species of *Cypris*. Several species are "remarkable among the Orchestidæ for their abnormally developed epimeral and tergal spines." These and the species of *Gammarus* from Lake Baikal will be referred to again later in this paper. It is simply desired here to indicate that these variations in *Achatinella* and *Allorchestes* have arisen from a single parent stock, within a small geographic province. The natural interpretation seems to be (*a*) that the environment is favorable, as evinced from the great number of individuals; (*b*) that this has favored and increased the growth force; and (*c*) that, finally, the law of multiplication of effects, reproductive divergence,[67] the survival of the unlike, and the conservative forces of natural selection and heredity have directed the growth force, and produced the specific differentiation which is now found.

A factor of Evolution, called "Reproductive Divergence" by Vernon,[67] seems to be operative here, since it affords an explanation for a means of differentiation in a single stock under a common environment. As this factor has but recently been discussed, it may well be defined at this time, so as to enable a direct application to be made. Reproductive divergence assumes that in many species there will be greater fertility between individuals similar in color, form, or size, than between individuals not agreeing in these respects, and that in subsequent generations, the divergence will become progressively greater in respect to the characteristic in question, so that finally the original stock will become separated into distinct varieties, sub-species, or species.

When, from any cause, the forces of nutrition are directed toward spine production, and when the direct results are accomplished in the reciprocal formation of one or more spines, there is often an apparent inductive influence or impulse given to growth toward the further production or repetition of spines. This may result in the formation of compound spines, or a group of spines, or even produce a generally spinous condition.

Naturally, spines arising through growth force may be useful for defense and offense, and the selective influences of sex and mimicry may also tend to greater development and elaboration. Furthermore, growth forces reacting on any external structures, as lines, lamellæ, ribs, nodes, etc., may tend to differentiate such ornaments into spines.

Therefore, under the general consideration of spines produced through growth force, the following factors are offered for consideration:

B. *From Growth Force.*

B 1.—Prolonged development under conditions favorable for multiplication.

B 2.—By repetition.

B 3.—Progressive differentiation of previous structures.

B 4.—Secondary development through the selective influences of defense, offense, sex, mimicry, and other external demands.

C. *External Restraint.*

Intermittent stimulus, as previously shown, produces growth in the direction of function. When the growth equals the waste, an equilibrium or static condition is reached, and no relative change occurs. The absence of either extrinsic or intrinsic stimulus will not be favorable to growth, and under such conditions, an organ or structure may remain undeveloped, or, if already present in the organism, it may waste away and degenerate into a vestigial structure, or even disappear altogether.

On the other hand, it is well known that continuous pressure not only prevents growth, but in addition resorption takes place, and in this way, the whole or a portion of a structure may be removed. These changes have frequently been studied in embryos, as well as in many internal structures, and are also familiar in the enlarged pedicle openings of many Brachiopods, caused by pressure of the pedicle, and in the similar opening for the byssal plug of *Anomia*. Packard[54] gives examples among the Crustacea and Insects, which are clearly to the point. He says of the Crustacea, "It may here be noted that the results of the hypertrophy and overgrowth of the two consolidated tergites of the second antennal and mandibular segments of the Decapod Crustacea, by which the carapace has been produced, has resulted in a constant pressure on the dorsal arches of the succeeding five cephalic and five thoracic segments, until as a result we have an atrophy of the dorsal arches of as many as ten segments, these being covered by the carapace."

The restraint of the environment through unfavorable conditions is the antithesis of A, or the influence of constructive external stimuli, and is considered as the extrinsic operation of destructive agencies. It is evident that external unfavorable conditions will repress growth, with a resultant atrophy of the structures affected. In this way, also, the environment may cause the disuse of an organ, which by consequent suppression may dwindle away to a spine, as in the leaves and branches of desert plants, and the spurs of the Python[39] representing the hind limbs. It may likewise repress growth, as in the spines on the lower side of the poriferous coral, *Michelinia favosa*,[40] representing aborted attempts at budding, the failure being due to the unfavorable position of the buds for securing food.

The restraint of the environment may also act in a mechanical manner to produce spines, as will be shown subsequently in some Brachiopods and Trilobites. Furthermore, spines arising through any phase of external restraint, may secondarily come under the influences of natural selection, and be useful for protection and offense, or conform to other external demands.

Under the head of external restraint, therefore, are the following categories:

C. *From External Restraint.*

C 1.—Restraint of environment causing suppression of structures.
C 2.—Mechanical restraint.
C 3.—Disuse.
C 4.—Secondarily for protection, offense, etc.

D. *Deficiency of Growth Force.*

The growth force in organisms may be reduced in several ways, the most general and obvious modes being by an unfavorable environment, lack of physiological plasticity, too close interbreeding, pathologic influences, and parasitism. The first commonly implies a scarcity of food, or it may be that the temperature, moisture, light, elevation, or other conditions are unsuitable to the normal development. The lack of physiological plasticity affects growth force by its resistance to change, and is most strongly apparent in highly specialized forms. The effects of close interbreeding in reducing vitality are too well known to require farther notice.

Only in exceptional instances can individual pathologic conditions have any effect on a stock. The retrogressive series of animals which are diseased in appearance, and are considered by Hyatt[34] as akin to pathologic distortions, are apparently types which have ceased to advance physiologically, and are therefore only adapted to special sets of conditions. In these, the pathologic or abnormal condition is racial instead of individual, and its cause seems to be a deficiency of vital power combined with great external differentiation, the final result being the assumption of characters belonging to second childhood and ending in extreme senility, with the loss of spines and other ornaments.

The life history of parasitic organisms shows their origin from higher normal types by a process of retrogression through loss of motion and disuse of parts. Their mode of living implies dependence upon the vitality of an immediate host, and altogether they may be deficient in the energy of growth force.

Any of the preceding factors, single or combined, acting upon an organism or group of organisms will produce suppression of structures or functions. Whether from external or internal causes, the waning and disappearance of characters are almost always inversely to the order of their development or appearance, either in the race or in the individual, and the most primitive or axial characters are therefore the most persistent and the last to disappear. In this way, a leaf may be suppressed into a spine representing the midrib, a branch into a spiniform twig, a leg or digit into a spine, etc. As in other primary causes of spine genesis, there may also come secondary influences of protection, offense, etc., controlled by natural selection.

It will be convenient to consider spine production from lack of growth force under three heads:

D. *Deficiency of Growth Force.*

D 1.—Intrinsic suppression of structures and functions.
D 2.—Disuse.
D 3.—Secondarily for protection, etc.

[To be continued.]

ART. XXVI.—*The Origin and Significance of Spines: A Study in Evolution;* by CHARLES EMERSON BEECHER.

[Continued from page 136.]

Summary of Causes of Spine Genesis.

Before taking up in more detail the various causes of spine development, and illustrating them by means of examples drawn from a number of classes of organisms, it is well to restate the factors which are believed to induce spine growth. This is especially desirable from the fact that, through the operation of unlike forces, similar conditions may produce the same morphological results, as in the differentiation of ornamental lamellæ and ridges, which, either from external stimuli or dispersion of growth force, may develop into spines. In such cases, it is difficult or impossible to distinguish the primary force, and the only satisfactory method is to discuss the subject under one head.

By carrying out this plan, and indicating the instances where the causes may replace or overlap each other, it may be shown how spines have originated, as follows:—

I. In response to stimuli from environment acting on most exposed parts. (A_1.)
II. As extreme results of progressive differentiation of previous structures. (A_2, B_3.)
III. Secondarily, as a means of protection and offense. (A_3, B_4, C_4, D_3.)
IV. Secondarily from sexual selection. (A_4, B_4, C_4, D_3.)
V. Secondarily from mimetic influences. (A_5, B_4, C_4, D_3.)
VI. Prolonged development under conditions favorable for multiplication. (B_1.)
VII. By repetition. (B_2.)
VIII. Restraint of environment causing suppression of structures. (C_1.)
IX. Mechanical restraint. (C_2.)
X. Disuse. (C_3, D_2.)
XI. Intrinsic suppression of structures and functions. (D_1.)

To illustrate the various causes of spine growth, representative examples which are believed to conform to the requirements will be selected from various groups of organisms. The number of spinose forms is so great that it will be impossible to give more than the briefest citation of a few of the leading types, especially those which have come under the notice of the writer; on this account the number of examples derived from the vegetable kingdom will be necessarily few.

I. *In response to stimuli from the environment acting on most exposed parts.* (A_1.)

The action of external stimuli falling on the most exposed parts of organisms is probably one of the most fundamental and fertile causes of spine production, since the relation between cause and effect is more direct and apparent here than by other modes of origin. In a general way, it comprehends all the remaining causes coming under the head of external stimuli, but for present purposes, it will be restricted by the elimination of secondary conditions, such as the indirect production of spines through differentiation of previous structures, and the action of external forces of selection.

The ruling forces in plants being so largely vegetative, or those of growth, and the cause of variation being principally physico-chemical and not molar, most of the modifications to produce spines will fall under other categories of origin (B, D) than the one now under discussion.

In the free swimming forms, however, as the Desmids and Diatoms, the external relations are found to be very much like those of animals. The frustrule of the Diatom, *Attheya decora*,[47] is quadrate in outline, and from the angles there extend sharp spinous processes, as represented in figure 32. The frustrule of the Desmid, *Staurastrum cuspidatum*, is composed of two triangular halves, and the spines project from the vertices of the angles. Other species of *Staurastrum*, *Xanthidium*, (*X. armatum*[47]), *Arthrodesmus* (*A. octocornis*[59]), etc., show similar spine growth from the most prominent portions of the frustrules. It is evident that in forms like these having angular outlines, any growth produced by external stimuli will naturally be greatest at the points of these angles, and in conformity with the previous analyses of these factors, a spiniform extension of the tissues would result.

Among the fresh-water Rhizopoda belonging to the Protoplasta (= *Amœbina*), the genus *Difflugia* affords good examples. *D. globulosa*[41] has a nearly spherical shell. In *D. pyriformis*,[41] the shell is elongate pear-shaped, and generally round on the summit or fundus, though in rare instances a central spiniform elevation is developed. This tendency becomes fixed in *D. acuminata*[41] in which the shell in general form resembles the preceding species, but the fundus is commonly prolonged into a single acuminate process (figure 33), though occasionally two or three spines are found. In *D. corona*,[41] there is a circlet of spines around the margin of the fundus besides the primary one in the center. *Difflugia constricta*[41] is a variable form, with the top of the shell generally smooth, though sometimes it is acuminate, and occasionally it has two or even a cluster of spines (figures 34–36). *Euglypha mucronata*[41] has a terminal spine, as in *Difflugia acuminata.*[41] *Placocista spinosa*[41] is a flattened miter-shaped form with a distinct edge, along which are numerous spines. It should be noted that no spines are developed on any portion of these fresh-water Rhizopods except those here mentioned.

The Nasellarian Radiolaria furnish many instances of a terminal spine from the summit of the silicious helmet or cup-shaped skeleton, as in *Eucyrtidium elegans*,[74] *Podocyrtis Schomburgki*,[74] *Tridictyopus conicus*,[26] *Cornutella hexagona*,[26] etc. Many of the primary, or axial, spines in other sub-orders probably originated according to I. In the Spumellarian forms especially, the principal spines project from the prominent portions, as in *Trigonactura triacantha*,[26] *Hymenactura copernici*,[26] *Rhopalastrum triceros*,[26] *R. hexaceros*,[26] etc. The existence of similar non-spinose species shows that the formation of spines is independent of the growth of the normal prominences, as in *Rhopalastrum malleus*,[26] *R. hexagonum*,[26] etc.

In the Foraminifera, the configuration of certain forms is such that parts of the test are much more prominent than others, and in these exposed situations, the spines are most frequently developed. Some of the triangular Textulariæ have spines at the two lateral angles on the oral side. Some of the individuals of *Textularia folium*[9] show that similar spines were developed at different stages of growth, so that, in a full grown specimen, there may be two or three pairs of spines along the sides. Others, like *Verneuilina spinulosa*[9] and *Colivina pygmæa*,[9] develop spines from the points of each chamber. A number of species, also, show a single spine at the apex of the shell, as *Pleurostomella alternans*,[9] *Bolivina robusta*,[9] *Polymorphina sororia*, var. *cuspidata*,[9] etc. In the latter species, the ordinary form is rounded, or obtusely pointed at the fundus.

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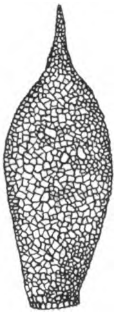

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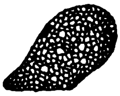

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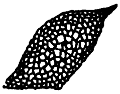

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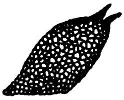


FIGURE 32. *Attheya decora*, a Diatom with spines from the angles. (From Mic Dict.)

FIGURE 33. *Difflugia acuminata*, a fresh-water Rhizopod, showing spiniform projection of the fundus. × 200. (After Leidy.)

FIGURE 34. *Difflugia constricta*, a fresh-water Rhizopod, with rounded fundus. × 175. (After Leidy.)

FIGURE 35. The same, showing a single spine on the fundus. × 175. (After Leidy.)

FIGURE 36. The same, showing two spines. × 175. (After Leidy.)

Some of the Infusoria have terminal spiniform processes, which, by analogy with other forms, have probably developed according to I, as *Ceratium tripos*,[9] *C. longicorne*,[9] *C. fusus*.[9]

The apertural spines on some of the Graptolites are on the most exposed portions of the hydrotheca, as in *Monograptus spinigerus*,[62] *Dicranograptus Nicholsoni*,[62] *Retiograptus tentaculatus* and *Graptolithus quadrimucronatus*. In many compound corals, the corallites are polygonal from crowding, and the most exposed portions, the angles of the calices, often bear spines, as *Favosites spinigerus*,[30] *Callopora exsul*,[30] etc. The spines on the septa and costæ of corals probably originate by intrinsic forces (B), since they are internal growths not influenced directly by external stimuli.

The spines on the ventral sacs of Crinoids are usually terminal, and in the most exposed situations; as in *Scytalocrinus validus*,[69] *Dorycrinus unicornis*,[69] *Aulocrinus Agassizi*,[69] etc.

The anterior and posterior pairs or rows of spines on the loricæ of some species of Rotatoria are in the most exposed places; as in *Anuræa squamula*, *Noteus quadricornis*, etc. The spinules on the tubes of *Spirorbis* are usually developed after it rises above the object of support so as to be exposed on all sides; as *Spirorbis spinuliferus*.[61]

The spinules at the corners of the angular cell apertures of many Bryozoa are in the most exposed situations, and probably arise through external stimuli; as in *Trematopora echinata*,[30] *T. spiculata*,[30] etc. The large marginal spines of the Brachiopod *Atrypa hystrix*[31] probably owe their excessive development to external stimuli, though the phylogeny of the species shows that the spines first originated through the differentiation of the radiate and concentric ornaments.

In many Pelecypods, the siphonal region receives a great amount of stimulus, and the post umbonal slope is the part most exposed. Along this slope are found many of the spines, and generally the greatest differentiation of ornament. Examples of spines on post-umbonal slopes may be seen in *Callista sublamellosa* and young *Saxicava arctica* (figure 27). Such spines represent periodic extensions of the mantle border, and in some cases, the stimulus for this growth may come from internal causes. The spines on *Unio spinosus* and related species are believed by Mr. Charles T. Simpson to assist in anchoring the shell in the sand of swift running streams. In *Callista*, the young *Saxicava*, and the Unios mentioned, the spines occur on all individuals and at such an early period as to preclude any special sexual function.

In the Gastropoda, the periodic extension of the shell over the posterior canal and the spiniform prominences formed on the labrum are situated in exposed places, or where the amount of stimulus is greatest; as in *Trophon magellanicus*, *Strombus pugilis*, *Fusus colus*, *Clavatula mitra*, *Melo diadema*, etc.

The spines on the larvæ of geometrid moths are usually on top of the loop, and are explained by Packard[64] as follows:

"The humps or horns arise from the most prominent portions of the body, at the point where the body is most exposed to external stimuli."

When the origin and function of spines in a great many forms of animals, and especially among the higher classes, are examined, it seems almost impossible to decide whether a spine has been originated and perpetuated by free variation and heredity, or by the general action of external stimuli on the most exposed parts; and in the latter case, whether or not under the selective influences of use. Its origin in either instance may be through external stimuli, but in the latter, it falls under other captions than A_1; or, in other words, the external stimuli excite the growth force at certain points, and the growths so produced may be simply reciprocal without function or they may serve purposes of protection or offense. Thus, the dorsal and rostral spines on the zoëa of the Decapods are on the most exposed points, and seem to function as defensive structures. As soon as the legs become well developed or when the animal ceases to swim at the surface and hides among the stones, etc., at the bottom, these spines become reduced and are often succeeded by others. The spines of the adult are also usually efficient for protection, but owing to the change in form of the animal and change of habitat, the most exposed parts are different from those of the larva, and the spines are frequently developed where there were no larval spines; as in *Cancer irroratus*, *Callinectes hastatus*, etc. Again, the horned ungulates show in their habits of sport, fighting, defense, and procuration of food, that the exposed angles of the top of the skull are subject to the greatest number of stimuli, and there the horns are developed. The connection between external stimuli and growth is here most manifest, for it is impossible to imagine the action of free variation or simple growth force as resulting independently, in the evolution of horned out of hornless species in several suborders of mammals, and in every case determining the location of the horns on the prominent angles of the skull, whether on the nasals, maxillaries, frontals, or parietals.

It is well known that toads and frogs defend themselves by using the head as a shield, and the cranial angles thus receive the greatest amount of stimulus. "There are natural series of genera measured by the degree of ossification of the superior cranial walls" (Cope[10]). In the highest genera, the head is completely encased, and in some forms the projecting angles are developed into short horns. The so-called "Horned Toad" (*Phrynosoma*) has the same habit of defense, and it is believed that this mode of protection or of receiving impacts has given rise to the structure, by stimulating growth at these points.

II. *As extreme results of progressive differentiation of previous structures.* (A_2, B_3.)

The differentiation of existing ornamental structures into spines has already been noticed in several instances in this article. It was shown that spines often arise by the elongation of nodes and tubercles or similar structures, by rhythmic alternating areas of growth in lamellæ and ridges, and by the growth of matter at the intersections of lines, lamellæ, ridges, etc. Furthermore, it was indicated that this progressive differentiation could be produced either (*a*) by the direct action of external stimuli affecting the amount of nutrition brought to a certain structure, (*b*) by the stimulus and dispersion of growth force, or (*c*) by a combination of the two forces. In this differentiation of the features which are generally called "ornamental," it will also be shown that the spine is the final result of progressive differentiation and, as previously indicated, can be formed out of a variety of other structures. The term "ornamental" is mainly one of human interpretation, and is used simply in apposition to "plain" or "simple"; for example, a clam cannot be imagined as consciously favoring a particular kind or arrangement of tubercles for ornamental purposes.

In a reticulate or cancellate surface formed by the crossing of raised lines, ridges, or lamellæ, it is evident that the causes or forces producing such structures will be increased at the points of intersection, and normally the amount of growth will here be greatest. In this way, it is possible to account for the very common presence of spines at the intersections of the radiating and concentric lines on many Mollusca and other organisms.

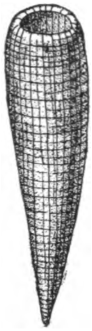
A few examples will now be given illustrating the differentiation of various structures into spines.

The points of intersections of the elements of the lattice in the Radiolaria are where spines are most frequently found; as in *Larnacalpes lentellipsis*, *Orosphæra Huxleyi*, *Carposphæra melitomma*, etc.[26] In *Xiphosphæra pallas*, the ridges about the openings or meshes are granular, and the intersections are raised into spines. Many of the discoid shells have their edges differentiated into spines, as *Heliodiscus asteriscus*, *H. cingillum*, *H. glyphodon*, *Sethastylus dentatus*, *Heliodrymus dendrocyclus*, etc. When an edge becomes elevated and defined as a carina, this structure is also often spiniferous, as in *Tripocalpis triserrata* and *Astropilium elegans.* The final differentiation of the radiate arrangement in the Radiolaria results in forms consisting only of a composite spine, as in the legion Acantharia.

In the Foraminifera, there are many instances of the gradual differentiation of carinæ, ribs, costæ, etc., into spines. In

Bulimina aculeata,[9] the surface nodes and granules become developed into spines. In *Textularia carinata*[9] and *Cristellaria calcar*,[9] the carinæ are spiniferous. The young of *Uvigerina aculeata*[9] is strongly costate, and later shell growth shows the costæ broken up into numerous spines. A related species (*U. asperula*[9]) has the whole test covered with spinules, which are sometimes arranged in lines, showing derivation from costæ. In *Truncatulina reticulata*,[9] the carina is made up of confluent spines, often discrete along the edge, and sometimes entirely separated.

37.



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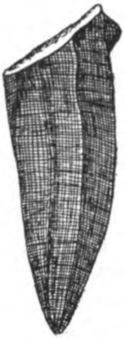

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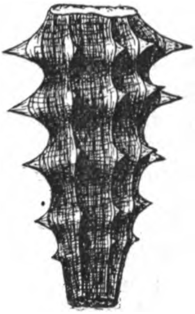

FIGURE 37.—*Cyathophycus reticulatus.* Ordovician. ⅓.
FIGURE 38.—*Dictyospongia Conradi.* Devonian. ⅓.
FIGURE 39.—*Hydroceras tuberosum.* Devonian. ¼. (Figs. 37, 38, 39, after Hall.)
To illustrate progressive chronogenetic and ontogenetic differentiation in a family of hexactinellid sponges.

The hexactinellid sponges belonging to the family Dictyospongidæ show some very clear instances of the progressive differentiation of ornament in time and in ontogeny. The Ordovician *Cyathophycus reticulatus*[28] is a turbinate form, with a rectangular mesh of longitudinal and transverse spicular rays (figure 37). At more or less regular intervals, some of the spicules are larger, thus dividing the surface into larger rectangular areas. In *Dictyospongia prismatica*[28] from the Devonian, the domination of eight of the longitudinal bundles of spicules has produced a prismatic form. *D. Conradi*[28] is regularly an eight-sided pyramid or prism when young, but with the growth and elongation of the sponge, it developed slight undulations, then nodes, and later prominent tubercles (figure 38). *Ceratodictya annulata* and *Hydnoceras nodosum*[28] show a further specialization in the formation of rings and nodes. Practically the limit to these specializations is attained in *Hydnoceras tuberosum*[28] (figure 39), *H. phymatodes* and related forms. In *H. tuberosum*, the apex representing the young stage or the initial growth is much like *Cyathophycus* or *Dictyospongia*. This is followed by a prismatic stage like *D. prismatica* and *D. Conradi*, then the nodes and tubercles are introduced and further growth produces the typical characters of the species. The tubercles are surmounted by a sharp spine formed at the intersection of two spicular laminæ, one concentric and one longitudinal.

Another type of surface specialization is shown in the genus *Physospongia* from the Keokuk group of the Lower Carboniferous. In this genus, there are bands of regular, alternating, elevated and depressed quadrules, the former frequently having the superficial layer of spicules extended into a spiniform process, as in *P. Dawsoni*.[28]

Among corals, there is occasionally some evidence of the external differentiation of structures into spines. The epitheca of the Tetracoralla frequently shows, by means of low lines or low ridges, the number and direction of the septa, and in some of the later species, these external septal lines are ornamented with rows of short spines or spinules; as in *Cyathaxonia cynodon*[18] and *Zaphrentis spinulosa*.[18]

Many Crinoids and Asteroids show the development of tubercles into spines, and the surface sculpture is often made up of ridges which bear strong spines at the points of intersection ; as in *Gilbertsocrinus tuberosus*,[69] *Technocrinus spinulosus*,[69] *Actinocrinus lobatus*,[69] *A. pernodosus*, *Oreaster occidentalis*, *O. gigas*, *Retaster cribrosus*, etc.

The concentric laminæ of growth in the Brachiopods are frequently differentiated into spinules; as in *Siphonotreta unguiculata*,[31] *Schizambon typicalis*,[31] *Spirifer fimbriatus*,[31] *S. pseudolineatus*,[31] *S. setigerus*,[31] *Cliothyris Royssii*,[31] etc. Other species show the differentiation of the radii into spines; as *Acanthothyris spinosa*,[74] and *A. Doderleini*.[15] In others the strong concentric laminæ passing over radii are often infolded into spines; as in *Atrypa spinosa*.[31]

Among the Mollusca, innumerable examples could be cited showing clearly the differentiation of various ornamental features into spines. Some of these have already been discussed, but may be referred to again in this connection. Thus, an illustration of the passage of concentric laminæ into spines is shown in *Avicula sterna*[36] and *Anomia aculeata*[36] (figures 26 and 28), and *Margaritiphora fimbriata*, etc. Many species of Gastropods show the same types of differentiation. The differentiation of radiating lines or ridges into spines is equally common, and is well shown in *Spondylus* (figures 12, 14, 30), and in *Lima squamosus* (figure 40). In

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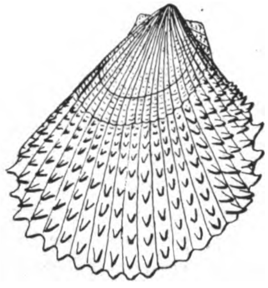


FIGURE 40. *Lima squamosus*. Natural size. To show differentiation of radii into spines.

most of these cases, the rib represents the progression of a fold in the edge of the mantle, while the spine is a process of a concentric lamina, and is usually more or less flat or tubular. Occasionally, the rib becomes obsolescent, and is represented by a row of spines, as in some specimens of the Gastropod, *Crucibulum spinosum.* When the radiating and concentric ornaments are distinctly continuous, a reticulate or cancellate appearance is produced, and the points of intersection often bear spines; as in *Aviculopecten scabridus,*[29] *A. ornatus,*[29] *Actinopteria Boydi,*[29] *Pterinopecten spondylus,*[29] etc.

The raised lines or ridges on the legs and carapaces of Crustacea are frequently spiniferous, as *Gelasimus princeps*, *Gecarcinus ruricola*, etc. The radii on the shells of barnacles are sometimes differentiated into spines; as in *Balanus tintinnabulum* var. *spinosus.*[18]

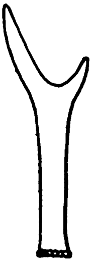
In the higher animals, the differentiation of ornamental features into spines is not common, especially as most of the forms are devoid of hard external parts. Among the fishes and reptiles, certain lines and ridges on the head and body are often spiniferous, while in others the scales have spiniferous ribs.

III. *Secondarily as a means of protection and offense.* (A_3, B_4.)

After spines have originated through the stimuli from the environment acting on the most exposed parts, or by growth force, or by progressive differentiation of previous structures, they may often acquire added qualities, one of which is to protect an organism from the attacks of many of its enemies.

Morris[49] shows that defense in animals is either mechanical or motor, while in the higher plants, it is purely mechanical. The spine clearly belongs to the mechanical mode of defense, and in many animals may be efficient without motion. If motion is added, it then may serve not only for protection but for offense as well. Natural selection evidently could not originate a spine, but after one has appeared from any of the causes mentioned in the preceding paragraph, this agency could tend to preserve and allow the spine to develop along certain lines. The restrictions as a defensive structure would be those of efficiency, and therefore all the monstrous growths, vagaries, and ornamental spine features would arise independently of the action of protective selection, and would be accounted for by the operation of the forces of the environment, growth, and sexual selection. In this way, the simple antlers of the Tertiary Deer may be imagined to have reached the highest degree of efficiency as weapons, by ordinary natural selection (figure 41). In most cases, the subsequent increasing complexity of the antlers during more modern times cannot have improved their usefulness for protection or fighting (figures 42, 43), and probably arose through gradual specialization according to the law of multiplication of effects, acted on by the agency of sexual selection. In some species, as the Reindeer (*Rangifer tarandus*), the differentiation of the antlers has secondarily produced a useful structure. One of the brow tines in this species has become greatly enlarged and palmated, and serves to assist in removing the snow to uncover food. Evidently this has had something to do with the common retention of the antlers in both sexes.

41.



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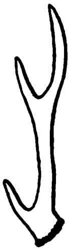

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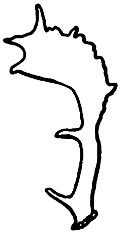

FIGURE 41. Antler of *Cervulus* (?) *dicranoceros*. Pliocene.
FIGURE 42. Antler of *Cervus pardinensis*. Pliocene.
FIGURE 43. Antler of the Fallow Deer (*Cervus dama*).
Reduced. (After Nicholson and Lydekker.)

Certain types of horns are common to particular regions, especially when the cattle are in a semi-wild state, as in the Western Plains of America. The Texas cattle have long, gently curved horns standing out from the head. Similar forms are prevalent in the cattle of southern Italy and in other warm temperate regions. Farther north, the horns become more curved in a direction parallel with the head, and are therefore closer to the skull. The most northerly representative of the hollow-horned ruminants, the Musk-Ox (*Ovibos mochatus*) has the horns hanging down close to the skull and only curved outwards in their distal portions. Marsh suggests to the writer that these variations in the directions of the horns have been influenced by the climate. A warm climate permits the horns to stand out directly from the skull. Farther north, or in a colder region, the frequent freezing of the horns and their consequent drooping has induced a natural drooping condition, and an Arctic climate has resulted in the production of horns closely appressed to the skull, in which position they cannot be affected by freezing temperatures.

Another possible service for antlers is also suggested by Marsh. As is well known, the male Moose is one of the most wary of the Cervidæ, and detects noises at great distances.

The large palmate antlers act as sounding boards, and, when listening, the animal holds his ears in the focus of the anterior surfaces of the antlers.

The hollow-horned mammals afford some of the most evident examples of the use of horns for protection and offense. In species with permanent horns, like the bison, oxen, goats, cattle, antelopes, etc., the horns are generally present in both sexes, though in the males they are often much the larger. In defense, many of the horned ruminants hold the head down, thus protecting the nose and bringing the top of the skull into prominence. In this position, the horns are most effective. A similar posture is taken by the horned batrachians and lizards.

The Porcupine and Echidna rely largely on the protection afforded by their spines, and on this account they are sluggish in their movements, and make little effort to escape approaching enemies.

Many of the great horned Dinosaurs of the Mesozoic are well provided with an armature of protective plates and spines on various parts of the body. In addition to an armature on the body, *Triceratops*[46] had three large horns on the head, one median (nasal) and two lateral (supra-orbital). These were powerful offensive and defensive weapons. There were also other small nodes and spiniform ossicles around the posterior crest of the skull and on the jugals, forming a part of the general armor. In *Stegosaurus*,[42] the efficient offensive and defensive weapons were the huge spines on the tail, and it is interesting to note as a parallel to this condition, that the greatest nerve centers were in the sacrum, and therefore posterior also.

No group of vertebrates shows such a variety of protective and offensive characters as the fishes. Many of the older types were heavily plated, while in others the fin-spines were greatly developed. Among modern forms, the protective character of the spines is well shown in types like the Spiny Box-fish, *Chilomycterus geometricus* and *Diodon maculatus*. A combination of mechanical and optical protection is afforded in the remarkable Australian Pipe-fish, *Phyllopteryx eques*[25] (figure 49). This fish has numerous spines and ribbon-like branching filaments, the former giving it a mechanical defense, and the latter assisting in its concealment among sea-weeds, to which it bears a striking resemblance.

Spines for protection are extremely common among insects, even in larval forms. They have been so frequently noted as to require no elaboration here. Packard[54] has ably discussed the origin of nodes, tubercles, and spines, among certain caterpillars. Among the forms which feed exclusively at or near the ground, he finds the body usually smooth, while those feeding on trees or on both trees and ground are often variously spined and tuberculated. These ornamental features arise from the modification of the piliferous warts common to all lepidopterous larvæ, and he concludes that the trees were more favorable for temperature, food, etc., than the ground, and that an increase of nutrition and growth force led to the hypertrophy of these warts into tubercles and spines. Having thus arisen, they immediately became useful for protection from birds and parasitic insects.

Among the Crustacea, there are also numerous examples of protective spines. These may be confined to parts of the body and legs especially exposed, or the entire animal may partake of the spiny character, as in the crab, *Echidnocerus setimanus*, where even the eye-stalks and antennæ are spiniferous. Others, like *Lithodes maia*, have the spines generally distributed over the carapace and legs. While serving for defensive purposes, this generally spinose character has probably reached its extreme development through the influence of repetition (B_3). The nauplius larva of *Lepas fascicularis* is very large, and has highly defensive spines which are explained by Balfour[3] as a secondary adaptation for protection. The larger spines on Trilobites, especially those from the genal angles and the axis, doubtless served protective purposes. The extremes of spinosity in this class are found in the various species and genera of the family Acidaspidæ, and also in many forms of *Arges*, *Terataspis*, *Hoplolichas*, etc.

Even among the star-fishes, which are so generally spinose, some forms have the spines so prominently developed on the most exposed portions of the animal that they evidently serve for protection; as *Acanthaster solaris*, *Echinaster spinosus*, etc.

The examples already given are sufficient to emphasize the fact that after spines are developed, they may then often serve for protection and offense and therefore be useful, their efficiency being controlled by natural selection resulting in the survival of the fittest.

Another process or kind of selection has been described by Verrill, as "Cannibalistic Selection." He has shown that the young of carnivorous animals often prey upon each other, as in the larval forms of some Decapoda, or sometimes even before the escape of the young from the egg capsules, as in some of the Gastropoda. Here, of course, any natural variation in the newly-hatched animals which would give an individual some advantage over its companions would tend to its preservation and to their destruction. In this way, it may occur that the relative growth of spines in the zoëa of decapods has determined the survival of the well-armed individuals, as in the zoëa of *Cancer*[68] (figure 44), *Carcinus*, *Homarus*, etc.

44.

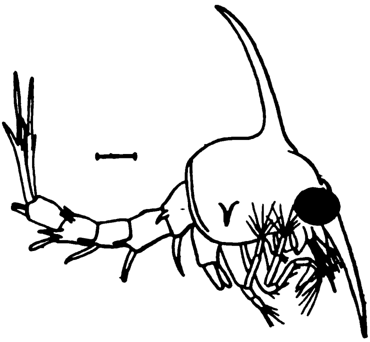

FIGURE 44. Zoëa of the common crab, *Cancer irroratus*; lateral view. × 8. (After Verrill and Smith[68].)

IV. *Secondarily from sexual selection.* (A_4, B_4.)

The males and females of so many animals present differences in size, color, and ornament, that corresponding variations in the development of spines, horns, and antlers, might naturally be expected. That such differences actually occur in nature is evident. Every gradation can be found between horns or antlers common to both sexes and those confined to one sex. Probably the initial difference is as ancient as sex itself.

Sexual variations of horns are most familiar among the mammals. Some, as the Giraffe, Ox, Bison, and Reindeer, have them present in both sexes, though the antlers of the female Reindeer are smaller and more slender than in the male, and in the American variety are sometimes absent. Others, as in the Prong-horn Antelope, many sheep, goats, etc., have the horns usually quite small in the female, and well developed in the male. Lastly, the modern Deer, Elk, Moose, etc., have the antlers confined to the males alone, the female being entirely without them.

Some of the early deer (*Procervulus*) seem to have had antlers in both sexes, and in nearly all the families of the Ruminata, there are species without horns, other species with horns in both sexes, and still others with horns only in the male. In the wild state, the presence or absence of horns and their character in any particular species seem to be well established, but in domesticated forms, the greatest variety is found. Among domesticated cattle, presumably of one species originally, varieties are found without horns, and others with horns, showing all degrees of twisting and length.

By protecting cattle from enemies, by forcing them into changed environment, and by varying amounts of nutrition, man has evidently brought the original stock into a condition of free variation. This state has been made use of in the production of endless varieties by selection and cross-breeding.

Darwin[14] accounts for the sexual selection affecting the growth of the antlers in the Deer as due to excess in the number of male individuals, and their struggles for supremacy in the possession of a mate. The antlers at the breeding season are strong and solid, and are therefore at their maximum of efficiency in each individual. They are shed at or before the time the young are born. Previous to the growth and maturity of the new antlers, the young are so far advanced as to be able to avoid being killed by the adult males. Furthermore, Darwin suggests that the excessive development of antlers into palmate and arborescent forms was probably an ornamental character attractive to the females. These complicated antlers not being the most efficient weapons, the fighting proclivities of the males would tend to favor the individuals with simple antlers, and to repress the more differentiated forms. Thus, the two influences would be opposed to each other, though not necessarily equal. The law of the multiplication of effects may also have some force, since it may carry a structure beyond the bounds of efficiency. Even in one of the oldest horned mammals, the *Protocerus*[46] of the Miocene Tertiary, a great difference is seen in the horns of the two sexes. The female has little nodes or tubercles, which in the male rise to the height and prominence of the horns on the Giraffe, or are even relatively more pronounced.

The males of some other vertebrates have spiniform processes or spurs on their legs and wings serving particular functions. The spurs in birds are to be considered mainly as weapons which are used by the males in combats among themselves. They are developed on the metatarsal or metacarpal bones as bony processes ensheathed in horn. In the females, the spurs are generally rudimentary. A kind of spur is also found on the hind limbs of the male *Echidna* and *Ornithorhynchus*, attached to the astragalus. It is perforated by a duct leading from a gland. The functions of the spur and of the secretion are unknown.

Many lizards especially among the Chamæleons present striking differences between the sexes, and the males of some of them develop veritable horns like those in cattle, sheep, and other hollow-horned ruminants. Darwin[14] illustrates and describes a number of most interesting examples. One of them (*Chamæleon Oweni*) is here shown (figures 45, 46). The male has three horns, one on the snout and two on the forehead. They are supported by bony excrescences from the skull. From the peaceable nature of these animals, Darwin concludes that "we are driven to infer that these almost monstrous deviations of structure serve as masculine ornaments."

The males of the tropical American genus of fishes, *Callichthys*, "have the spines on the pectoral fins stronger and longer than those of the female, the spine increasing in size as the male reaches maturity" (Seeley[65]).

Among insects, the males of many beetles belonging to the Lamellicorns have long horns arising from various parts of the head and thorax. One of the best known forms is the Hercules beetle (*Dynastes hercules*). Bateson[6] states that, in this and other genera, it is commonly found that the males are not all alike, but some are of about the size of the females and have little or no development of horns, while others are more than twice the size of the females and have enormous horns. These two forms of male are called "low" and "high" males, respectively. Among the males, similar dimorphism in respect to size and length of horns occurs in *Xylotrupes gideon*, and in the stag beetle (*Lucanus cervus*, *L. titanus*, *L. dama*).

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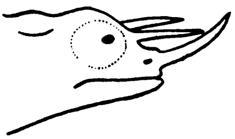

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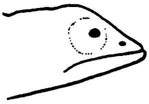

FIGURE 45. Profile of head of *Chamæleon Oweni*; male. $\frac{1}{3}$.

FIGURE 46. Female of the same species. $\frac{1}{3}$. (After Darwin.)

In many of these cases, the horns are evidently protective and not developed through the selective influences of the female. In such cases, the habits of the male are supposedly different from those of the female. Thus, Wallace[70] suggests that the horned males of the coleopterid families Copridæ and Dynastidæ fly about more, as is commonly the case with male insects, and that the horns are an efficient protection against insectivorous birds. These interpretations clearly do not come under the definition of sexual selection as restricted to the choice of either sex. Beauty, voice, or strength, may influence the selection of a mate by the opposite sex, but when the habits of the sexes are different and certain characters arise in response to this change, the explanation is then really found in the law of adaptation or physical selection.

V. *Secondarily from mimetic influences.* (A_5, B_4.)

Natural selection may aid in furthering and preserving a spinose organism after the spines have originated through any primary cause. One aspect of this influence may be treated under the head of mimicry. If, by their resemblance in form, color, or voice any characters are similar to characters present in the surroundings of the animal, and afford a means of protection or are useful, they may be considered as mimetic in the broadest sense of the term. Mimicry is usually restricted to a kind of special resemblance, and not to the cases of general resemblance afforded by an animal without significant colors in general harmony with its surroundings.

The influence of mimicry in the production of spines can only occur where the object mimicked is spiniform or spinose. Apparently this is rather infrequent and of little real importance as a factor of acanthogeny.

Insects and spiders have furnished the greatest number and variety of mimetic forms, both in their larval and adult conditions, and naturally would be expected to furnish examples of spines having mimetic significance. The object mimicked may be another species of insect or animal, in which case, there is usually some offensive or defensive quality rendering the resemblance useful to the mimicker; or, the whole or a portion of some plant or other object may be imitated, tending to the more or less complete concealment of the mimicking insect.

Satisfactory examples are not at hand, though doubtless many occur in nature, and some have been described, but not for the present purpose. A few will be cited here which seem to conform to the requirements.

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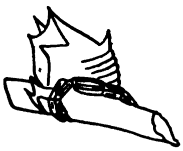

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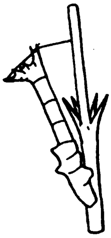

FIGURE 47.—Profile of a Spider (*Cærostris mitralis*) on a twig mimicking a spiny excrescence. (From Peckham, after Vinson.)

FIGURE 48. The larva of the Early Thorn Moth (*Selenia illunaria*) resting on a twig; showing mimicry of stem and spiniform processes. ½. (After Poulton.)

A Madagascar spider (*Cærostris mitralis*) is described by Elizabeth G. Peckham[56] as sitting motionless on a branch and resembling a woody excrescence with projections or spiniform processes, figure 47. Other spiny spiders of the Epeiridæ probably have similar protective mimetic features, as *Epeira spinea* and *Acrosoma arcuata.*

The larva of the Early Thorn Moth as described and illustrated by Poulton[58] bears a strong resemblance to the twig upon which it rests, even to spiniform processes, axils, and buds (figure 48). Packard[64] cites a striking case of mimicry in the caterpillar of another genus of moth (*Schizura*), where the spines and tubercles resemble the serrations of a leaf "so that when feeding on the edge of a leaf, the Schizuræ exactly imitate a portion of the fresh-green serrated edge of a leaf including a sere, brown, withered spot, the angular, serrate outline of the back corresponding to the serrate outline of the edge of the leaf."

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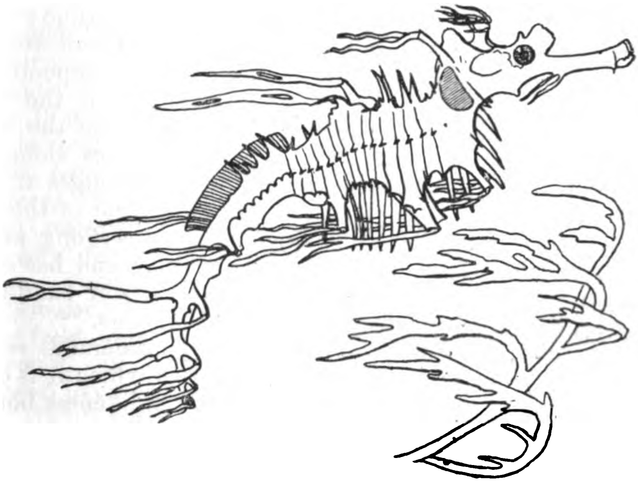

FIGURE 49. Australian Pipe-fish (*Phyllopteryx eques*) and frond of sea-weed in lower right hand corner; showing mimicry. ½. (After Günther.)

The Australian Pipe-fish *Phyllopteryx*, previously mentioned under the head of spines for protection, shows the mimicry of a plant by an animal to a striking degree. This fish closely imitates a seaweed (figure 49) and Günther[25] gives the following description of the spines and filaments on the species *Phyllopteryx eques:* "There is a pair of small spines behind the middle of the upper edge of the snout, a pair of minute barbels at the chin, and a pair of long appendages in the middle of the lower part of the head. The forehead bears a broad, erect, somewhat four-sided crest, behind which there is a single shorter spine. A horizontal spine extends above each orbit. There is a cluster of spines on the occiput, and from these narrow appendages are prolonged. On the nape of the neck is a long spine, dilated at the base into a crest, and carrying a long forked appendage. The back is arched, and on the under side are two deep indentations. The spines on the ridges of the shields are the strongest; they are compressed, are not flexible, and each terminates in a pair of short points. There is one pair of these spines in the middle of the back, and one on each of the three prominences of the abdominal outline; they terminate in flaps, which are long and forked. There are also very long compressed flexible spines without appendages, which extend in pairs along the uppermost part of the back, while a single series extends along the middle line of the belly. Small short conical spines run in a single series along the middle line of the sides, and along the lateral edges of the belly; and there is a pair of similar spines in front of the base of the pectoral fin. The tail, which is about as long as the body, carries the dorsal fin; it is quadrangular, and has sharp edges. It carries along its upper side five pairs of band-bearing spines, which terminate in branching filaments." *

The Horned Toad *Phrynosoma* bears considerable resemblance to the joints of the Prickly Pear, with which it is often associated, and it may be suggested that the likeness both in form and spinescence represents mimetic characters.

VI. *Prolonged development under conditions favorable for multiplication.* (B_1.)

The prolonged development or existence of a stock under favorable conditions for multiplication may be considered as one of the primary influences favoring the production of spines. This implies abundance of nutrition and comparatively few enemies outside of other individuals of the same or closely related species. Under a proper amount of increased nutrition, the vitality and reproductiveness of a stock are raised, and other things being favorable, it is found that the stock will give expression to what has already been described as free variation. Hypertrophy is also very apt to be one result of abundant nutrition, so that structures of little or no use may be developed, and some of them comprise certain features which are often called ornamental.

In the excessive multiplication of individuals, it is evident that there must be a great number of natural variations, and that some of these will affect the pairing of the sexes in such a manner as to accentuate and delimit certain variations. Eventually, there also comes a struggle for existence in which favorable modifications have a decided advantage. In this way, it is believed that the great amount of differentiation found in some isolated stocks has been brought about. Primarily then, a favorable condition for nutrition is assumed, which is followed by excessive numerical multiplication; while the natural variations are augmented and governed by the action of reproductive divergence for which such conditions are favorable. Secondarily, these variations are subjected to the influences of cannibalistic selection, defense, offense, sexual selection, and mimicry.

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* The artist who copied Günther's figure for Lennis "Synopsis der Thierkunde," 3d ed., by H. Ludwig (vol. i. p. 770, 1883) connected the fish with the adjacent fronds of seaweed so as to form a single organism.

In illustration of the amount of differentiation attained by a single stock under favorable conditions, the Amphipod Crustaceans, *Gammarus* and *Allorchestes*, found in lakes Baikal and Titicaca, respectively, may again be noticed.

In respect to the number of species, *Gammarus* is very sparsely distributed over the world, though in Lake Baikal alone a hundred and seventeen species have been described by Dybowsky.[17] In contrast to this, it may be mentioned that but four fresh-water species have been discovered in the whole of Norway. In Lake Baikal, all the depths explored (to 1373 meters) have furnished species. Those living near the surface are vividly colored, yet apparently make no attempts at concealment. Many of the species are also highly spinose, though not sufficiently armed to be protected from the fish. As these Crustaceans are voracious creatures, the spinose character has probably been favored by the agency of cannibalistic selection. The lake has a number of species of fish for which the Gammaridæ furnish excellent food, but the presence of a species of seal, predaceous fish, as well as the native fishermen keep the fish below the danger point, thus allowing the Gammaridæ to become very abundant.

Similarly, in Lake Titicaca, there is a wonderful specific development of a kindred Crustacean, *Allorchestes*. One of the most spinose species (*A. armatus*) is also the commonest, and according to Faxon[19] occurs in countless numbers (figure 50).

Packard[54] shows that, among certain moths, the caterpillars as soon as they acquired arboreal habits met with favorable conditions in respect to food, temperature, etc., and that as spines and tubercles arose by normal variation, such features being found useful for protection, were therefore preserved and augmented.

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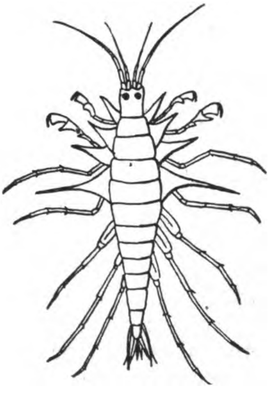


FIGURE 50. *Allorchestes armatus*. A spiny amphipod from Lake Titicaca. Female; dorsal view. Natural size = 9mm. (After Faxon.)

The differentiation of *Achatinella* has already been discussed (p. 132) as affording a striking instance of free variation among the Mollusca. The evolution of the Tertiary species of *Planorbis* at Steinheim, as described by Hyatt,[18] furnishes another example, though in neither case has the differentiation of structures proceeded far enough to result in spines. The costate form (*Planorbis costatus*) was tending toward that end, but did not attain it.

The series of Slavonian *Paludina* in the Lower Pliocene, as elucidated by Neumayr and Paul,[50] show a somewhat further advancement. The species in the lowest beds (typus *Paludina Neumayri*) are smooth and unornamented. Higher in the strata, they are angular and carinated, and at the top of the series, the shells are carinated, nodose, and subspinose (typus *Paludina Hœrnesi*). The living American genus *Tulotoma* is closely related to the most differentiated species (*P. Hœrnesi*), and its approach to spinose features is more pronounced.

Under the phylogeny of spinose forms (pp. 18, 19) an outline of the life history of the Brachiopod *Atrypa reticularis* and derived species was presented. This being one of the commonest types of Brachiopods in the Silurian and Devonian, often forming beds of considerable extent, it seems quite likely that its prolonged development under favorable conditions for multiplication must have had an effect on the amount and kind of variation.

It has been noticed by Brady[9] and others, that in the Foraminifera, *Globigerina bulloides*, *Orbulina universa*, etc., the pelagic forms comprise two varieties which are generally distinct, a spinous form and another with small minutely granular shells. The bottom specimens of the same species are also commonly without spines and often smaller. The interpretation seems to be that the large specimens indicate an abundance of nutrition which has also produced hypertrophy of the normal granules into spines. Some bottom specimens are large, but they are usually abnormal and of a monstrous or pathologic nature.

From the foregoing examples, the conclusion to be drawn is that, with full nutrition, there comes a numerical maximum, and naturally with this a corresponding number of normal variations. Some of these modifications, as spines, have arisen by hypertrophy. After having thus originated by growth force, they may or may not be of use for offense, defense, or concealment, or in any way give their possessor a distinct advantage.

[To be continued.]

ART. XXXIV.—*The Origin and Significance of Spines: A Study in Evolution;* by CHARLES EMERSON BEECHER.

[Continued from page 268.]

VII. *By repetition.* (B_2.)

UNDER the consideration of spine production by repetition, it is proposed to include local repetition or duplication of spines on or about a primary spine, the limit of this repetition resulting in a generally spinose condition.

It has been shown that intermittent stimulus produces growth, and furthermore that growth can only take place with proper nutrition. Under local stimulus, the currents of the circulation or forces of nutrition are set up in an organism toward the center of stimulation. The nutrient matter is brought to this point, and more or less of it is expended in building up a structure which is the reciprocal or direct resultant of the stimulus. Now, since all motion is primarily rhythmic,[68] and the repetition of parts an almost universal character among organisms,[6] it would appear that the foregoing conditions would be favorable to the repetition or reproduction of the structures. In this way, it is easy to account for the growth of spines that cannot be explained as the direct result of external stimuli (A), or by any process of decrescence (C, D). The nature of the influence seems to be similar to induction in electrical physics, or to the force or stimulus of example in human conduct.

Stated as a concrete case, a simple spine produced by any primary cause may be taken, and it will be granted that the vital or physiological adjustments produced in its growth and maintenance have brought about or induced an harmonic condition in the adjacent tissues. Subsequent growth will most naturally repeat the previous structures, so that in addition to the primary spine, there will be other smaller spines on or about it, together constituting either a compound spine or a group of spines.

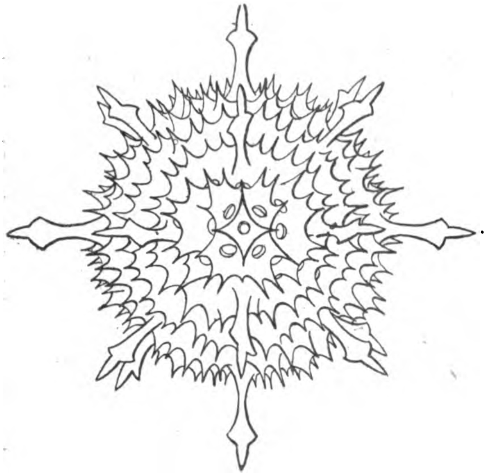
Carrying this repetitionary process to a maximum, there would result a generally spinous condition. As a possible illustration of this, no class of organisms probably exhibits so many kinds and series of repetitions of all sorts of external structures as the Echinodermata, and it is significant that this is a typically spiniferous sub-kingdom.

Except in a few classes of organisms, compound spines are relatively rare as compared with simple spines. They are very common among the Radiolaria, which furnish the greatest complexity occurring anywhere in the organic world. (See Plate

I.) They are also quite frequent among the Echinoidea, but more rare among the Asteroidea and Crinoidea.

Compound antlers are especially characteristic of the modern Deer family, though compound horns are but rarely found elsewhere among the mammals. The Prong-horn Antelope of America is the only living species of hollow-horned ruminant having this character. It, of course, is not intended that extra pairs of horns, which being separate, and often originating on different portions of the skull, should be considered as compound horns in the sense employed here. Likewise compound spines arising through suppression of organs or structures are not to be included here, as the compound thorns on the Honey-locust representing aborted branches.

51.



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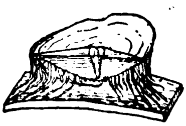

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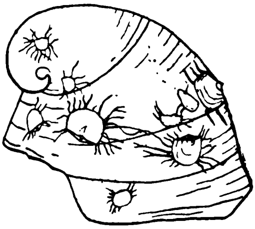

FIGURE 51. *Acontaspis hastata.* A Radiolarian, showing multiplication of spines by repetition. × 200. (After Haeckel.)

FIGURE 52. *Strophalosia keokuk.* An attached Brachiopod, showing the spines extending from the ventral valve to and along the surface of attachment. × 2.

FIGURE 53. A Gastropod shell (*Platyceras*) to which are attached a number of *Strophalosia keokuk.* Natural size.

The fin-spines of fishes are often compound, and sometimes are made up of several elements as in the spines of *Edestus* (*E. vorax*). Quite a number of Mollusca develop compound spines, as in many species of *Spondylus* and *Murex.* They are also not uncommon among the Crustacea and Insecta. Compound spines are infrequent in the Brachiopoda, being developed in but few species (*Spirifer hirtus*[31]). The Foraminifera also present but few examples (*Polymorphina Orbignii*[9]).

A number of generally or highly spinose types will now be noted to illustrate the limits of the repetition of spiny structures, the first spines having probably arisen through the operation of some primary cause, and the derived or secondary spines being produced, it is believed, by the law of repetition.

The Radiolaria have already been frequently mentioned, but as they are the most spiniferous of all classes of animals, and represent the highest degree of spine differentiation attained (figure 51 and Plate I), another brief notice will be of interest. These spines furnish characters of high taxonomic value, although generally speaking they seldom have more than specific importance among other classes. The Echinoidea and Asteroidea must also be noticed in this connection, though from the nature and origin of their spines, they do not conform to the mode of spine growth in other classes.

Productus, *Productella*, *Strophalosia*, *Aulosteges*, and *Siphonotreta* represent highly spinose genera among the Brachiopoda. *Strophalosia* is a form in which the ventral valve is cemented to some object. Whenever the valve rises well above the object of support, the spines are free like those frequently present on the dorsal valve; otherwise the spines extend root-like along the supporting surface (figures 52, 53).

Aulosteges presents a still further tendency to complete spinosity, for not only are both valves covered with spines, but the deltidium also.

Spondylus (figure 30) and *Murex* are well-known types of very spiny forms of Mollusca. *Acidaspis*, *Terataspis*, etc., hold the same place among the Trilobita; *Echidnoceras*, *Lithodes*, etc., among the Decapoda; and the Spiny Box-fish (*Diodon*), Pipe-fish, etc., among the Pisces. The higher animals also furnish examples of extreme spinosity, as in the Horned-Toad (*Phrynosoma*), the genera of Ceratopsidæ, gigantic Cretaceous Dinosaurs, and the Echidna and Porcupine.

All these forms present numerous spines, some of which cannot be explained as having arisen directly from external stimuli, for they are in comparatively well-protected regions out of the way of external stimuli. Neither can all of them serve for offense and defense, as they are often not located in the most advantageous positions; nor are they differentiated out of any previous ornaments or special structures. In fact, no factor of spine genesis except the one of repetition seems to be sufficient to account for their development.

VIII. *Restraint of environment causing suppression of structures.* (C_1.)

The previous categories of spine production (I–VII) have been brought about by some process of growth or concrescence through external and internal agencies. There still remain for discussion the formation of spines by processes of decrescence caused by extrinsic restraint (C), or intrinsic deficiency of growth power (D). The lack of vitality or growth force generally stands so directly as the result of an unfavorable environment, that it is often difficult or impossible to distinguish between their action. Furthermore, as in the case of many parasites, it may be seen that the environment may be quite favorable as regards temperature, nutrition, etc.; but unfavorable in respect to motion and use of sensory and motive organs. From the almost universal degradation and retrogression of parasitic forms, it is necessary to consider these as intrinsically deficient, and therefore lacking in the qualities of growth force which normally favor a progressive evolution. Here, also, there are apparently two intimately associated causes. In an attached animal, the absence of stimulus from disuse of an organ tends toward atrophy, and the retrogressive development serves to affect many organs in the same manner. The direct and indirect results of the restraint of the environment may therefore be expected to shade imperceptibly into each other, with only the extremes sufficiently distinct for separation.

The influence of an unfavorable environment as effecting the character and growth of plants and animals is well shown in desert or arid regions, and the flora has been made the subject of especial study by Henslow.[33] In such regions, the first thing to impress the observer is the small size of the species. Next to diminutive size, the scantiness of life is a striking feature, for large areas are common in which life is almost wanting. An examination of these plants reveals a series of characters not usually present elsewhere, among which may be mentioned the development of a minimum amount of surface, constituting what is known as consolidated vegetation; next their uniform gray color, due either to excessive hairiness or a coating of wax; and lastly, their frequent spinescent characters.

The spines on desert plants are a feature of such general occurrence that it has led to the notion that vegetable spines are always associated with unfavorable conditions and are therefore suppressed structures. This is probably incorrect, for in plants as in animals, spines may be developed by the progressive differentiation of previous structures; as in the angular edges of the leaf-stems of many Palms becoming spiniferous; or, as will be shown, suppressed structures may arise from deficiency of growth force. In all cases, spines may or may not serve for protection. Thus, while they are not always an indication of unfavorable environment, those occurring on desert plants may generally be so considered, for they are developed out of structures which are normally of vital physiological importance.

An animal or plant having spines and living in a favorable environment, involving freedom of motion for animals, and abundance of nutrition without extremes of temperature or dryness for both animals and plants, will, it is believed from the discussions and analyses of spine genesis in its various phases, develop these features in most instances, without the sacrifice of organs and structures having important physiological and motor functions. Thus, ordinarily, among animals it is found that spines arise as excrescences or outgrowths of exoskeletal or epidermal tissues, without seriously affecting the function of the organ or organs upon which they are located. Such cases may clearly belong to the most progressive series, and in fact usually occur there.

On the other hand, if it is found that a leg, a wing, a digit, or other organ is developed into a spine, this is always accomplished by a process of retrogression, resulting in the greater or lesser suppression of the part in question. It is also seen that this kind of spine occurs most frequently in retrogressive series or in others showing arrested development, and the necessary interpretation seems to be either that the environment is or has been unfavorable, at least so far as the particular organ or set of organs is concerned, or that the vital power has declined. Both influences are intimately associated, and the latter is often the direct result of the former.

The stunting effects of aridity and barren soil on our common plants is familiar to all. Among the plants of the desert is found every evidence of similar stunting combined with adaptations to resist the unfavorable conditions of deficient water supply, excess of radiation, etc. The diminution in size applies not only to stature, but to the leaves and branches, especially the parenchymatous tissues or parts of the plant engaged in aëreal assimilation. Consonant with these changes, the drought and other conditions produce a hardening of the mechanical tissues, which is of great aid in resisting the extreme heat and dryness of the desert. Sometimes a deposit of wax affords a similar protection.

The reduction of the leaves takes place in various ways. They may simply become smaller in every dimension and finally be reduced to mere scales, or an aphyllous condition may be established. They may grow narrower and narrower until only the hardened veins or midrib remains; or leaves may be developed only for a short time, and, in the case of compound leaves, after the shedding of the leaflets, a spiniform leaf axis remains, as in *Astragalus Tragacantha*[38] (figures 55, 56). The suppression of branches tends towards the same end;

namely, either to their complete disappearance or to their partial suppression into hard spiniform processes or thorns. Thus, both leaves, branches, and other parts of the plants may become reduced to their axial elements, bringing about what is commonly termed spinescence.

The spiny character of these plants is therefore one of the results of an arid environment, and it may or may not be of sufficient frequency to give an especial character to a particular desert flora. There is, moreover, a secondary influence which has an effect in determining the abundance of spinose plants in desert as well as in many other situations. This relates to the destruction of the edible unarmed species by herbivorous animals, and the comparative immunity of the spiny types. Thus, in old pastures, the prevailing flora is apt to be one that is offensive to grazing animals. This character is generally given by poisonous plants or those having a disagreeable flavor, or by those whose form or spiny structures afford protection.

This secondary influence by grazing animals may have had some effect in determining the particular abundance of spiny plants in certain desert regions, and their comparative infrequency in other similar regions. In either case, the unfavorable environment brings about a suppression of structures, and one type of this action results in the production of spines. These represent the limits of retrogression before the part becomes entirely obsolete.

Wallace has criticised Henslow's views on the origin of xerophilous plants and their distribution. It is believed that the views here offered remove some of the objections, and bring the opinions of these authors into greater accord.

Under arid conditions, bracts, stipules, leaves, and even branches may become spinescent. Some forms in which the spinose character has not as yet become permanently fixed by heredity, when transported or found living in moister and richer soils, develop normal leaves or branches, and lose their spinescence; others, like the Cactus, retain their spines under similar changes; while still others, as *Acanthosicyos horrida*,[33] cannot be artificially cultivated, and have become truly xlerophilous types.

As examples of plants which lose their spines by cultivation, the Pear, species of Rose, Plum, etc. (Henslow), may be cited. According to Henslow,[33] others, as *Onomis spinosa*, have an especially spiny variety (*horrida*) living on sandy sea-shores, while in more favorable natural situations, the same plant becomes much less spiny, and under cultivation loses its spines. M. Lothelier[42] also found that by growing the Barberry (*Berberis vulgaris*) in moist air, the spines disappeared, the parenchyma of the leaves being well formed between the ribs and veins. Dry atmosphere and intense light both favored the production of spines.

Henslow[33] cites the genus *Zilla* as a desert plant in which the branches are transformed into spines, *Echinops* for a similar modification of the foliage, *Fagonia* for spiniform stipules, and *Centaurea* for spinescent bracts. As further illustrations taken not only from desert plants but also from others commonly found in dry, rocky, or unfertile situations, the following examples may be taken, some of which are familiar cultivated species. The stunting of branches into spines is common among neglected Pear and Plum trees, and is a normal character in the Hawthorn, Honey-locust, *Cytisus* (figure 54), *Vella*, etc. Leaves transformed into spines are characteristic of the Cactaceæ of America, the columnar Euphorbiaceæ of Africa and southern Asia, and are also familiar in the half-shrubby Tragacanth bushes (figures 55, 56) so common in southern Europe, especially in the eastern portion, and in the ordinary Barberry (figure 13). Spiniform stipules are usually present in the species of *Robinia*, of which the Common Locust (*Robinia pseudacacia*) furnishes a well-known illustration (figure 57). Spiniform bracts are best known among the Thistles (*Cirsium lanceolatum*, *C. horridulum*, etc.).

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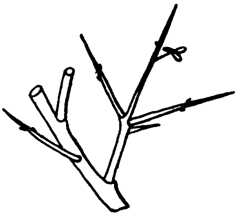

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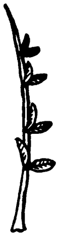

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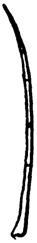

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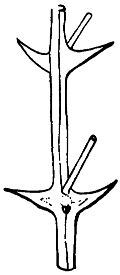


FIGURE 54. The spiny *Cytisus* (*C. spinosus*), showing suppression of branches into spines. (After Kerner.)

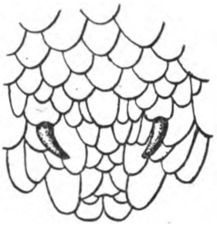
FIGURE 55. A single leaf of Tragacanth (*Astragalus Tragacantha*) from which the three upper leaflets have fallen. (After Kerner.)

FIGURE 56. Leaf axis of the same, from which all the leaflets have fallen. (After Kerner.)

FIGURE 57. Twig of Common Locust (*Robinia pseudacacia*), showing spines representing stipules.

As the restraint of an environment acting on an animal so generally results in the disuse and atrophy of the organs affected, most cases will have to be considered under the head of disuse. Therefore, while the environment is the primary factor, its influences are mainly exhibited through secondary or resultant conditions. In some cases, however, it is possible to interpret a vestigial or suppressed structure directly into terms of an unfavorable environment. Thus, if the probable origin of the vestigial hind legs of a Python is considered, it leads to the belief that they represent legs which were of functional importance to some of the early ancestors of this snake. The gradual elongation of the body and the consequent change from a walking or direct crawling habit to a mode of progression chiefly by horizontal undulations, necessarily brought the legs into a relation with the environment which was unfavorable either for their function or growth. Their suppression is complete in most snakes, but in the Python, the hind legs are represented by two spurs or spines (figure 58). On the interior of the body they are supported by vestiges of femora and ilia, showing their true affinities with hind limbs. Some snake-like Batrachians (as *Amphiuma* and *Proteus*) still retain short and weak external limbs. These would undoubtedly soon be lost by a change from aquatic to terrestrial or arboreal habits.

58.



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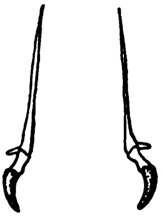

FIGURE 58. Portion of skin of Python, showing the spurs which represent the suppressed or vestigial hind legs. × $\frac{1}{3}$. (After Romanes.)

FIGURE 59. Bones of suppressed legs of Python. All but the claw-like termination are internal. × $\frac{1}{3}$. (After Romanes.)

In explanation of the nodes and spiniform processes on the epitheca of *Michelinia favosa*, it may be suggested that they represent aborted corallites, or attempts at budding. This coral belongs to the order Porifera, which has been shown by the writer[7] to have very pronounced tendencies toward proliferation, and on the interior of the colony, these attempts result in the production of mural pores. Most of the species of *Michelinia* are hemispherical or spherical. *M. favosa* is inclined to be pyriform in shape, rising above the object of support, and thus presenting a rather large epithecal surface. Manifestly the lower side of the corallum is unfavorably situated for the growth of corallites, and any efforts at proliferation on the part of the peripheral corallites is apt to result in stunted outgrowths. There is here a very close connection between restraint of environment and deficiency of growth force. If the whole corallum is taken into consideration, the restraint of the environment may be taken as preventing the growth of corallites on the lower side. If one of these single stunted corallites is considered, it may be said that the deficiency of growth force through lack of nutrition caused its suppression.

IX. *Mechanical restraint.* (C_2.)

Among the factors of spine genesis, mechanical restraint is probably of the least importance. It can only rarely happen that an organism is forced to grow a spine contrary to the natural tendencies of normal development. Yet as there are occasional types of spiniform structures which can best be explained as due to the mechanical restraint of the environment, it is necessary to notice them in order to make the categories of origin as complete as possible.

The illustrations will be taken chiefly from the Brachiopoda and Trilobita. The recent Brachiopod *Mühlfeldtia truncata* is semi-elliptical in outline, and has a very short stout pedicle which holds the shell so closely to the object of support that the beak is truncated from abrasion and resorption. In specimens attached to a small branch of a coral, thus allowing the cardinal extremities of the shell to project beyond the object of support, the ends of the hinge are generally rounded. Specimens growing on a large flat surface have the cardinal extremities angular or submucronate. Similar variations are to be observed in other living species of Brachiopods (*Cistella*, some *Dallina*, etc.). Some of the extinct genera show more highly developed cardinal extremities which are often very characteristic of certain species, though considerable variation is found to exist. It is evident that these elongated hinge lines have arisen from the mechanical necessities of a functional hinge, and their greater or less extent is also to a degree dependent upon the nature of the object of support which furnishes a stimulus to the growing ends of the hinge. A marked example is shown in *Spirifer mucronatus*, with the cardinal angles extended into spiniform processes (figure 60). Similar features are presented by many other species of *Spirifer*, *Orthis*, *Leptæna*, *Stropheodonta*, etc.

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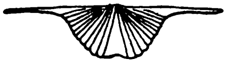
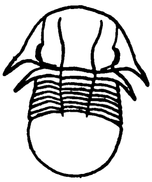


FIGURE 60. Dorsal view of *Spirifer mucronatus*, Devonian. Showing spiniform cardinal angles. × ½. (After Hall and Clarke.)

In the Trilobites, the pygidium, or abdominal portion, consists of a number of consolidated segments, and the segments of the thorax are successively added in front of this tail piece. The first thoracic segment is therefore formed between the cephalon and pygidium, and its form is mechanically in agreement with the requirements of the animal for bending the body, and with the adjacent margins of the cephalon and pygidium. In a way, it may be said that the segment is moulded by the adjacent parts, and may therefore take its form from the cephalon (figure 61), or from the pygidium, as in the examples following:

61



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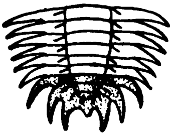

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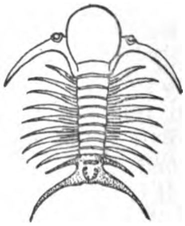

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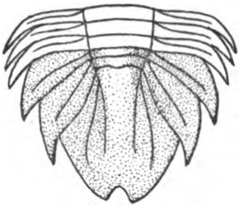

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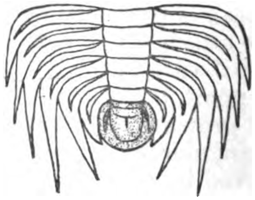

FIGURE 61. *Illænus* (*Octillænus*) *Hisingeri*, Ordovician, Bohemia. A Trilobite showing spiniform pleural extremities of first thoracic segment, corresponding to the genal spines of the cephalon. × $\frac{3}{4}$. (After Barrande[4].)

FIGURE 62. *Cheirurus insignis*, Silurian, Bohemia. Pygidium and six thoracic segments. × $\frac{3}{4}$. (After Barrande.)

FIGURE 63. *Deiphon Forbesi*, Silurian, Bohemia. Entire specimen showing spiniform pleural of segments corresponding in direction to those of the pygidium. (After Barrande.)

FIGURE 64. *Lichas scabra*, Silurian, Bohemia. Pygidium with three thoracic segments, showing spiniform ends of pleura. × $\frac{3}{4}$. (After Barrande.)

FIGURE 65. *Paradoxides spinosus*, Cambrian, Bohemia. Pygidium and six free segments. × $\frac{3}{4}$. (After Barrande.)

During growth, the new segments are added in front of the anal segment, so that after the number of abdominal segments is complete the thorax is increased by the successive addition of what in earlier moults were pygidial segments. By this means, the pygidium generally controls or determines the character of the segments of the thorax. If the pleura of the pygidium are extended into spiniform processes, the pleural ends of the segments are also spiniform, as in *Lichas* (figure 64), *Ceraurus*, *Cheirurus* (figure 62), *Deiphon* (figure 63), *Acidaspis*, *Dindymene*, etc.

Likewise, if the pleura or their distal ends are directed posteriorly nearly parallel to the axis, the mechanical necessities of motion require that the portions of the free segments pointing backward should be free, thus making the ends of the thoracic pleura generally appear as retrally curved spiniform extensions. Extreme examples of retrally directed pleura accompanied by small pygidia are shown in *Paradoxides* (figure 65), *Holmia*, *Olenellus*, *Elliptocephala*, etc. Genera having the ends only of the pleura directed backward are generally less inclined to form spiniform terminations. In contrast with these, it is found that all the Trilobites having the pleura directed outwards and with entire pygidial margins, do not ordinarily develop long pleural spines; as *Asaphus*, *Illænus*, *Agnostus*, *Phacops*, *Calymene*, etc.

The examples of the caterpillars of moths belonging to the Schizuræ, described by Packard[64] as mimicking the serrations of the leaves upon which they feed, have previously been noticed in this essay, under the head of mimetic influences. The initial cause of the spines may possibly be explained as in part due to the mechanical conditions. During their early existence the larvæ feed on the lower side of the leaves, and have no spines. Later they feed on the edges of the leaves, and at the same time acquire dorsal spines. The conformation of the animal to the serrated edge of the leaf would produce corresponding elevations and depressions on the back. The location of these would be fairly constant from the habit of the animal of feeding chiefly between the denser leaf veins which determine and terminate the serrations. The raised parts of the animal would receive the greatest amount of stimuli, and at these points spines would naturally appear.

The processes producing the spines noticed in this category (IX) are classed with others under decrescence, for the reason that the growth is restrained or controlled by mechanical necessities. If the restraint were absent, it is probable that a more expansive growth would take place or that other structures would be correspondingly benefited.

X. *Disuse.* (C_3, D_2).

In causing the reduction or atrophy of an organ, the effects of disuse have generally been recognized by most observers. In this way, the origin of many of the so-called "rudimentary organs" has been satisfactorily explained by Darwin[14] and others. Two classes of structures are evidently comprised within the common definition of rudimentary organs, namely, nascent and vestigial organs.

Nascent structures indicate the beginnings or initial stages of organs, while vestigial structures are the remnants left after the functional suppression of organs. The suppression is usually caused by unfavorable conditions or by disuse, which produce either a retardation of growth or a retrogressive development. In both cases, the results are similar. By retardation, an organ is prevented or restrained from functional development and is therefore useless as a normal organ. By retrogression, an organ gradually reverts to an initial type, loses its function, and becomes a vestigial structure. In most instances, a change of food or habit, or the substitution of a new and functionally higher structure, causes the disuse of some organ, which, under previous conditions, was of use to the animal.

Nascent structures, or the beginnings of organs, are generally made up of active tissues that only require stimulus and nutrition to perfect their function. On the other hand, suppressed or vestigial structures are composed of comparatively inert tissue and are in consequence largely made of the mechanical elements of secretion of the organism. It may therefore be considered that true rudimentary or nascent organs are potentially active, and suppressed structures are inert. It is with the latter class, the inert, that a study of spine genesis by atrophy is chiefly concerned.

The gradual loss of function through disuse, and the consequent loss of nutrition with the concomitant rapid decrescence of active tissues, brings about a change in the ratio of active and inert structures. The progression of this process naturally results in the production of a structure having a maximum of inert or mechanical tissues, and a minimum of active constituents. Moreover, it has already been shown that the axial elements are the most persistent, and therefore the last to disappear; also that the peripheral appendages and outgrowths of any organ first show the action of decrescence. Evidently, the conditions here described are favorable for the production of spines out of an organ primarily possessing distinct active functions. The axis of an organ gives the necessary form, and the hard tissue the structure, so that the whole will conform to the definition of a spine given early in this paper; namely, a stiff, sharp-pointed process.

The restraint of the environment was found to be one cause for decrescence of organs. Another, which is properly the subject matter of the present section, is disuse; and lastly, it will be seen how the deficiency of growth force may bring a similar suppression of structures.

There is considerable difficulty in selecting particular examples which will conform clearly to the strict requirements of these three categories. In a certain sense, some of the examples of spines produced by decrescence may belong to more than one category. However it does not prevent the acceptance of any one of the three as primary causes. Thus, it may be urged that disuse has caused the atrophy of leaves into spines among many desert plants, or produced a similar reduction of the limbs in a Python. While this may be true from one point of view, yet the manifest unfavorableness of the evironment in both, seems to be a sufficient reason for making it the primary factor. On the other hand, many parasites showing similar atrophies are not dependent upon a large number of active organs for their food and maintenance. After finding a host, an abundance of food is at hand, and the environment may be considered a favorable one. All the organs, except those of nutrition and reproduction, then become more or less useless and dwindle away, leaving vestigial organs, or disappearing altogether. Furthermore, a change of habit, as from climbing to flying, will necessarily cause the atrophy of some of the structures used for climbing, and the hypertrophy of others for flying.

Most of the examples illustrating the production of a spine through the atrophy of an organ by disuse are to be found in the legs and digits of animals. The process bears considerable resemblance to the formation of spines on many plants by the suppression of leaves, branches, etc. They will be noticed here, although properly these vestigial structures among animals are more strictly of the nature of claws, or at the most, spurs.

Many parasitic plants, especially among the Balanophoreæ, are reduced to a simple stem bearing the inflorescence. The leaves are represented by scales which are often spiniform, though seldom of sufficient stiffness to entitle them to be called spines. In desert plants, many of which have a similar type of growth, the hardening of the mechanical tissues by the effects of drought has converted similar leaf structures into spines, while the parasitic plants are not normally subjected to such continuous dryness and extreme heat, and therefore the mechanical tissues seldom become hardened.

Parasitic animals, especially among the Crustacea and insects, often show a reduction in the number of joints in the legs, and even in the number of limbs themselves. The terminal claws generally persist, and are sometimes longer than the rest of the leg; as in the Itch mite, *Sarcoptes Scabei*, and in the female of the parasitic Copepod *Lernæascus nematoxys* (figure 66).

Among many aquatic Crustacea and Limuloids, the specialization and seggregation of the ambulatory and swimming appendages towards the head or anterior regions of the body have produced a corresponding suppression of appendages on or near the extremity of the abdomen. This statement of fact is the basis of the principle of cephalization of Dana,[12] who applies it especially to the Crustacea, as follows: "There is in general, with the rising grade, an abbreviation relatively of the abdomen, an abbreviation also of the cephalothorax and of the antennæ and other cephalic organs, and a compacting of the structure before and behind; a change in the abdomen from an organ of great size and power and chief reliance in locomotion, to one of diminutive size, and no locomotive power." Audouin's law that among the Articulata, one part is developed at the expense of another, may be also noticed here as affording a further explanation of the suppression of the posterior appendages correlative with the greater development of the parts anterior to them. In a Crustacean using its tail for propulsion, as the Lobster (*Homarus*), the telson is broad and flat, and the adjacent segment has a similar development of the appendages. In other forms, as the Horse-Shoe Crab (*Limulus*) and the Phyllocarids, the tail is not used for propulsion, and at best serves chiefly as a rudder, while some of the legs on the anterior part of the abdomen or on the thorax are large and strong and are often provided with paddles. These groups, the Limuloids and Phyllocarids, show a greater or less suppression of the last abdominal appendages, and in many genera, the body terminates in a spiniform telson or tail spine. The process of suppression may or may not result in a spine. In the crabs, the abbreviated abdomen is folded under the cephalothorax, and in *Lepidurus* and *Pterygotus* the telson is a scale or plate-like organ. For the most part, however, the abbreviation of the abdomen and the suppression of its appendages have reduced the telson to a spine, as in *Limulus* (figure 67), *Eurypterus*, *Stylonurus*, and *Prestwichia* among Limuloids; and *Olenellus* among the Trilobites. In addition to a telson spine, the Phyllocarids have two lateral spiniform cercopods, the three spines together constituting the post-abdomen, as in *Ceratiocaris*, *Echinocaris* (figure 68), *Mesothyra*, etc.

Although the last abdominal segments of the Horse-Shoe Crab have lost their appendages and show evidences of suppression, yet the tail spine is a large and useful organ, for it is of just the proper length to enable the animal to right itself after being overturned, which it is unable to do with its feet alone. The process of natural selection has doubtless in this way contributed to the development and retention of the long spine. This use cannot be ascribed to the tail spines of the Phyllocarids, though they evidently were important aids in directing movement, and also offered some degree of protection.

The terminal claws on the phalanges of the wings of some birds are nearly all that remains of the external fingers, or digits. In the Hoactzin of South America (*Opisthocomus cristatus*), the young bird has a thumb and index finger, both provided with claws, and climbs about much like a quadruped, using its feet, fingered wings, and beak. According to Lucas,[43] a rapid change "takes place in the fore limb during the growth of the bird, by which the hand of the nestling, with its well-developed, well-clawed fingers, becomes the clawless wing of the old bird with its abortive outer finger." Similar claws or spurs occur on a number of other birds, some having functional wings, as in the example just described, and others having only vestiges of wings, as in the Wingless Bird of New Zealand (*Apteryx*, figure 69).

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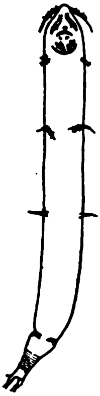

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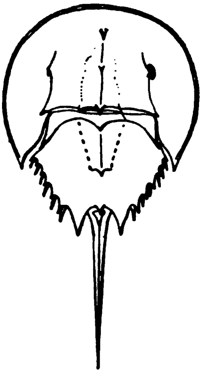

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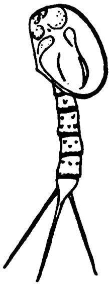

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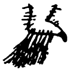

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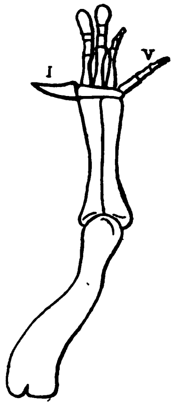


FIGURE 66. Female of *Lernæascus nematoxys*. A parasitic Copepod, showing suppression of limbs. Enlarged. (After Claus.)

FIGURE 67. Horse-Shoe Crab, *Limulus polyphemus*, showing telson spine and abbreviated abdomen. Reduced.

FIGURE 68. A Devonian Phyllocarid, *Echinocaris socialis*, showing spiniform telson and cercopods.

FIGURE 69. Wing of *Apteryx australis*. × $\frac{1}{3}$. (After Romanes.)

FIGURE 70. Skeleton of right fore limb of the Jurassic Dinosaur, *Iguanodon bernissartensis*, showing suppressed first digit. × $\frac{1}{30}$. (After Dollo.[16])

Another example may be taken from the Dinosaurian Reptiles. The Jurassic genus *Iguanodon*, from England and Belgium, belongs to a group (Ornithopoda) in which the number of functional digits varies from three to five in the manus, and from three to four in the hind feet. In this genus, the hind foot had three functional toes, representing the second, third, and fourth of a normal pentadactyl foot. The first is represented by a slender tarsal bone alone, while the fifth is completely suppressed. The manus, or fore foot, of this animal shows the second, third, fourth, and fifth digits of functional importance as digits, while the first is shortened and atrophied to the condition of a stout spur, standing out at right angles to the axis of the leg, as shown in figure 70. The fore legs of *Iguanodon* and others of the same order were short, and apparently used more for prehension than locomotion, and in *Iguanodon*, the suppression of the pollex, or thumb, into a spur doubtless provided the animal with a powerful weapon. Here is seen the suppression of a digit by loss of normal function, resulting in a protective structure of considerable value.

XI. *Intrinsic suppression of structures and functions.* (D_1.)

The most obvious and direct relationship between an unfavorable environment and the suppression of structures to form spines was afforded by desert plants. In illustration of the intrinsic suppression of structures by deficiency of growth force, the vegetable kingdom again seems to offer the clearest evidences of a like relation between cause and effect. Instead, however, of taking an unfavorable environment, in the present instance a favorable environment must be assumed, and then a type which expresses in various ways its deficiency of growth force must be sought.

In the desert plants, it was found that no single family exclusively constituted the desert flora, but that a considerable variety of types were present, and that some of these belonged to perfectly normal families commonly living under ordinary favorable conditions. Moreover, it was evident that there were certain types of form and habits of growth which were especially characteristic of plants living in desert or similar unfavorable regions. Therefore, to illustrate clearly intrinsic restraint or suppression of structures, it will be necessary to take an environment which, in most respects, may be considered as favorable, and also a type of plant life presenting evidences of a deficiency of growth force.

The great groups of plants commonly known as brambles and climbing plants appear to meet most of the requirements. They abound in regions where the greatest luxuriance of vegetation is found, and are therefore chiefly characteristic of the tropics. Kerner[38] estimates that there are two thousand species of the true climbing plants in the torrid zone, and about two hundred in temperate regions. Tropical America has the largest number of species, the flora of Brazil and the Antilles being especially rich. In the sombre depths of the tropical forest, the climbing plants, or "lianes," are not so abundant as in the open glades and along the edge of the forest, where the amount of light is greater and the conditions of existence more favorable. As far as richness of soil, amount of light, and degree of temperature are concerned, it must be admitted that their environment is as favorable as that of any of the associated plants having different habits of growth. The difference between the strong and erect plants and the comparatively weak and climbing forms is therefore not an extraneous one. It resides within the plant structures themselves, and is an intrinsic character or an expression of hereditary vital forces.

The law of recapitulation demands that each individual during its development shall pass through an epitome or recapitulation of its ancestral history. In view of the fact that the young seedlings of climbing plants and brambles have the erect form and proportions of normal erect foliage stems, it is safe to infer that they have been derived from erect forms. Further evidence is afforded from the absence of climbing plants in the earlier terrestrial floras. It is obvious, therefore, that they have been developed out of erect forms by a process of degradation.

The next striking feature to be noticed in climbing plants is their extreme slenderness, due to the general suppression of the plant body. They may attain lengths not reached by the highest trees, and yet the diameter of the trunk is but a minute fraction of the length. The Climbing Palm, or Ratan, has stems of great length and tenuity. It has been stated that stems two hundred meters long have been observed having a uniform thickness of only from two to four centimeters.[18] The diameter of such a stem would be only one or two ten-thousandths of its length. The length of the internodes is another conspicuous character in climbing plants, and both this and the slenderness of the stems suggest the results obtained by growing ordinary plants in the dark, where the conditions are adverse to increased vitality.

The transfer of function from one part of the plant to another, usually by a process of retrogression or degradation, is also very common. The first growth above the ground is a leafy stalk. Later, after the plant has attained a considerable height, the lower portion puts out quantities of rootlets and loses its foliage. The rootlets may be mere dry threads or points of support for the stem; or, if they happen to encounter a crevice containing soil, they develop into true absorbent organs. In others, the ends of the growing stems or any point on the stems, upon reaching the earth, may put out vigorous roots. These facts seem to show a lack of positive differentiation throughout the plant, which admits of the substitution of a lower structure for a higher, by the suppression of a higher function.

Lastly, the general spininess of climbing plants and brambles is a well-known and conspicuous character. Kerner[38] says that "most, if not all, plants which weave into the thicket of other plants are equipped with barbed spines, prickles and bristles." These spiniform processes seem to fall naturally into two classes. First, those produced by the suppression of stipules, leaves, petioles, branches, etc., and second, those appearing as simple eruptions on the surface.

71 72 73

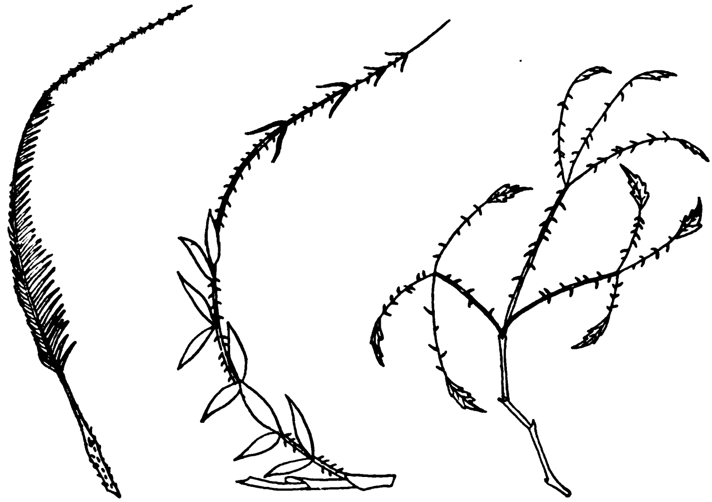


FIGURE 71. Leaf of Ratan, *Dæmonorops hygrophilus.* Reduced. (After Kerner.)
FIGURE 72. Leaf of Ratan, *Desmoncus polyacanthus.* Reduced. (After Kerner.)
FIGURE 73. Bramble, *Rubus squarrosus.* Reduced. (After Kerner.)

The suppression of normal plant organs into special structures, as tendrils and claspers, is extremely common, and, as already shown, this process if carried far enough without complete suppression will favor the production of a spiniform growth representing the axial elements of the organs. The classes of organs thus affected are practically the same as those in desert plants, though varying somewhat in manner and degree. The consolidated type of plant body is naturally absent, for, in this respect, the diffuseness of climbing plants is quite antithetical. It does not seem necessary to give a long list of examples among the climbers, illustrating the suppression of organs into spines. Although apparently not of rare occurrence, spines produced in this way are not as common as among desert plants. Two figures of the pinnate leaves of Ratan are introduced here to show the suppression of a number of the terminal leaflets into spines (figures 71, 72). In *Machærium* the stipules are converted into thorns.[62] A tropical *Bigonia* (*B. argyro-violacea*) has normal full-sized simple leaves, and suppressed leaves bearing two opposite leaflets on one stalk, and ending "in a structure which divides into three limbs, with pointed hooked claws, and which is not unlike the foot of a bird of prey."[38]

By far the greater number of spines on climbing plants are of the nature of prickles, and are not produced by the suppression of any particular organ or organs, but appear usually without any very definite order. They represent outgrowths of the superficial layers, and hypertrophied plant hairs, or trichomes. The cause of these cortical eruptions is not clear, although they seem to be intimately connected with the general suppression of the plant body. They are therefore a secondary and not a direct result of suppression. Bailey[2] asserts that, "probably the greater number of spinous processes will be found to be the *residua* following the contraction of the plant body." This connection is very apparent in the consideration of the suppression or contraction of various plant organs, but is less obvious when applied to the surface of the whole plant, though doubtless it is the true explanation. In continuation of this idea, it may be suggested that the prickles represent aborted attempts on the part of the plant, through hereditary influences, to recover its former normal proportions. Or, they may exhibit the action of the law of repetition acting in an organism where the initial cause of spine production is the intrinsic suppression of such structures as leaves, petioles, stipules, etc. The subsequent repetition of spines on other parts of the organism results in a series of homoplastic spines which are not homologous with those first formed.

The prickles on climbing plants and brambles may often serve for purposes of protection (D_3), and enable the plant to cling to a support, but these utilitarian properties cannot be considered as an initial cause. Natural selection, also, probably has fostered the development of certain types of spiny climbers and the production of adaptive characters. Nevertheless, in studying these forms, it is necessary to revert to the original consideration of the localized suppression of normal plant structures, and to the general suppression of the plant body as affording a more primary conception of the causes and modes of spine growth among climbing plants.

In many cases of retrogressive series of animals, there seems to be a close parallelism with some of the characters observed among the climbing plants. If the Ammonite family during the Cretaceous, or near the close of the Mesozoic, is taken as an example, it cannot be said that the environment of these old age or pathologic series is unfavorable in respect to food temperature, etc., for with them are associated many vigorous progressive series of other organisms. Neither can it be said, that in many cases the animals perished on account of over-specialization, though this was evidently the cause of the extinction of a large number. The return to a condition of second childhood in old age cannot be called a progressive specialization, since it clearly points to a deficiency of growth force.

Old age types, or phylogerontic forms, among animals may show the same attenuation or suppression of the body as do climbing plants. Thus, *Baculites*, considered by Hyatt as a typical phylogerontic type, has a very attenuate shell, and some species, after attaining a certain diameter, cease to increase in any direction except length. On account of being a chambered shell, it is manifest that the growth of the animal must have practically ceased, while its secretive activities were continued and confined largely to lengthening the shell. Other related genera of Cephalopods show a similar attenuation of the shell, evincing a stoppage of growth in the animal. Among the Mollusca, it seems quite likely that attenuation of form often accompanies decreased growth power.

The pathologic varieties of the Steinheim *Planorbis*, as described by Hyatt,[35] or of the recent *Planorbis complanatus* described by Piré,[57] are further illustrations of this attenuation accompanying the uncoiling of the shell. The sedentary *Magilus*, immersed in its coral host, is also an example, for not only does the shell cease to increase in diameter, but the whole interior, except a small cavity at the end, is filled with a solid deposit of lime. Similar examples could be multiplied indefinitely. Since, however, but few of them are spiniferous, their consideration does not properly come within the scope of the present discussion, though, as is well known, some of the attenuate forms often enlarge and contract periodically, such enlargements frequently leaving prominent laminæ or nodes that are sometimes differentiated into spines. They suggest the observations on growth, senescence, and rejuvenation, made by Minot,[48] who showed that in guinea pigs from a very early age, the increments of growth are in a steadily decreasing ratio to the increase of weight of the animal. This led to the general conclusion, that the whole life of an individual is a process of senescence or growing old.

Spines arising by a real pathologic or diseased condition of the individual can have little or no effect in producing a normal spiniferous variety or species. However, some note should be taken of them, especially as they may be congenital, and thus appear through several generations. In the human species, the peculiar skin-disease known as ichthyosis sometimes produces spiniform excrescences, and the victims are commonly called "porcupine-men." The most celebrated instance was the Lambert family. Haeckel[20] gives the following account of this family: "Edward Lambert, born in 1707, was remarkable for a most unusual and monstrous formation of the skin. His whole body was covered with a horny substance, about an inch thick, which rose in the form of numerous thorn-shaped and scale-like processes, more than an inch long. This monstrous formation of the outer skin, or epidermis, was transmitted by Lambert to his sons and grandsons, but not to his granddaughters. The transmission in this instance remained in the male line, as is often the case." Other similar examples are cited by Gould and Pyle,[21] and the disease is described as "a morbid development of the papillæ and thickening of the epidermic lamellæ."

CATEGORIES OF INTERPRETATION.

Having thus far examined the factors governing the origin of spines, and found that they could be grouped into a number of distinct categories, it is now desirable to interpret these results, and endeavor to arrive at the real significance of the spinose condition.

The two main generalizations which will be discussed are, first, that spinosity represents the limit of morphological variation, and second, it indicates the decline or paracme of vitality.

Spinosity a Limit to Variation.

A number of data have already been given, leading to the belief that, on becoming spinose, organisms have reached a limit of morphological variation. They may continue to develop more and more differentiated and compound spines, but no new types evolve out of such a stock.

The subject may be treated in two ways, both leading to the same conclusion. First, the stages and processes involved in the growth of a spine itself may be studied, and next the development of spines in the ontogenies and phylogenies of animals and plants may be examined.

The growth of a spine has already been described, and it was shown that this type of growth may arise from specialization of other ornamental features, such as nodes, ridges, and lamellæ, and also from the decadence of leaves, legs, etc. These observations and numberless others which could be made will be sufficient to show that almost any kind of superficial structure, as knobs, tubercles, ridges, laminæ, reticulations, etc., has by differential growth been changed into spines; also, that organs of various kinds, as legs, branches, leaves, etc., have by atrophy been reduced to spines. In each case, the parts in their development pass through the various intermediate stages, and clearly show that the spine is a result and not a mean. Moreover, none of these structures or organs is developed through the contrary process; namely, that of beginning with spines and passing through stages corresponding to laminæ, ridges, tubercles, etc. The spine is the limit, and out of it no further structure is formed.

It is necessary to make some mention here of the movable spines of Echinoderms, which appear to form an exception to the foregoing statements. There seems to be no doubt that the fixed and movable spines, the pedicillariæ, the paxillæ, and the spheridia are homologous structures, and that all begin as spiniform skeletal outgrowths, which by subsequent growth and modification produce the structures mentioned (Agassiz[1]). The echinoderm skeleton, including spines, etc., is deposited in the midst of living tissue, and in the case of the spines cannot be directly correlated with the spines of other classes of organisms, which are either very deficient in vitality or are dead structures as soon as completed. After the movable spines of echinoderms are fully developed, the living portion is often confined to the base, and the shaft becomes simply a dead structure upon which encrusting organisms may find lodgement, a condition seldom occurring in the living spines. These finished spines never develop into anything else, and are the structures which conform to the present discussion. The embryonic condition of the spines and pedicillariæ shows that they are really more internal than external structures, and therefore remain under the full control of the ordinary processes of growth, resorption, and modification by living tissues. Furthermore, the movable spines are of such functional importance that no close homologies can be made with ordinary spines found in other classes of organisms.

In tracing the ontogeny of a spinose form, it has been found (pp. 14–17) that each species at the beginning was plain and simple, and at some later period, spines were gradually developed according to a definite sequence of stages. Usually after the maturity of the organism, the spines reach their greatest perfection, and in old age, there is first an over-production or extravagant differentiation followed by a decline of spinous growth, and ending in extreme senility with their total absence.

There are abundant reasons for believing that the radicles of groups are undifferentiated and inornate, and whenever a class has had a long existence, it has been by the continuance of such radical types or by the development of secondary or tertiary radicles, which, though differing in internal characters, still retain a primitive simplicity in superficial features. The early stages of ontogeny of any form should agree with the radical stock, and, as already noted, these stages are simple. Hyatt[34] says on this point: "the evidence is very strong that there is a limit to the progressive complications which may take place in any type, beyond which it can only proceed by reversing the process, and retrograding. At the same time, however, the evidence is equally strong that there are such things as types which remain comparatively simple, or do not progress to the same degree as others of their own group. Among Nautiloidea and Ammonoidea these are the radicle or generator types. No case has yet been found of a highly complicated, specialized type, with a long line of descendants traceable to it as the radicle, except the progressive; and all our examples of radicles are taken from lower, simpler forms; and these radicle types are longer-lived, more persistent and less changeable in time than their descendants."

A few examples will now be taken from the life histories of large groups. In the Brachiopods, the order Protremata, containing most of the spinose forms, has 4 genera and 22 species in the Cambrian of America, 20 genera and 173 species in the Ordovician, and 30 genera in the Silurian. "Then began a steady decline, with extinction in the Carboniferous of North America. In the Triassic of Europe this order is sparingly represented by small species, and is there essentially restricted to the family Thecidiidæ, which continues to have living representatives in the Mediterranean Sea" (Schuchert[64]). The superfamily Strophomenacea of this order is the longest lived and excelled in amount of specific differentiation, there being 608 species in North America alone (Schuchert). In this superfamily the early families and genera were without spines, it being only when *Chonetes* is reached that the first spines are found in the order. In this genus, they are along the hinge, and seem to make up for the weak and obsolescent pedicle. Greater spine growth occurs in the genera *Productella* and *Productus*, where, in extreme cases, the surfaces of both valves are thickly studded. During the Carboniferous, the spiny Productii attained their maximum both in number, length of spines, and in individual size, for here occur the largest species of all Brachiopods. This was the climax. The Permian genera are chiefly degenerate forms (*Aulosteges*, *Strophalosia*), and with the close of the Paleozoic, the family Productidæ became extinct. The order Protremata, to which this family belongs, likewise underwent a rapid decline, and only two simple types continued on into the Mesozoic, while but one declining representative is living at the present time.

Among the Ammonites, the chief spiny forms are those occurring just before the final extinction of the group and representing the beginning of the decline of the order (*Crioceras*, *Toxoceras*, *Ancyloceras*, *Hamites*, etc.). In the Dinosaurian Reptiles, the great horned forms, *Triceratops*, *Torosaurus*,[19] etc., mark the extinction of the entire order. The great horned mammals of the Eocene, the Dinocerata, have left no descendants, and the giant Brontotheridæ, after undergoing various horn modifications through the Miocene, continued no further.

It is not desirable, however, to convey the impression that the spines or horns are alone responsible for this wholesale extinction. It has been shown that they are undoubtedly often an expression of extreme specialization, and generally they represent the limits to which superficial structures may be differentiated. Although there may be other expressions for similar conditions, yet the presence of spines is one, if not the most evident, marker of the attainment of these limits. The presence of a spine on an organ or part indicates the limit of progression or regression of that part or organ. If the spinose condition is general, or if it dominates important functions, it then indicates the limit of progression and regression of the organism.

Spinosity the Paracme of Vitality.

The physiological interpretation of spinosity is a correlative of the morphological aspect of the same condition, and, as it was found that spinosity was a limit to morphological progress or regress, it will now be shown that it also indicates the paracme or decline of physiological progress. Both inferences are drawn from the individual or ontogenetic standpoint, as well as from the racial or phylogenetic.

In the spinose individual, the decline of vitality has been studied by Geddes[20] in thorny plants. He concludes that they show a "gradual death from point backwards (i. e. *ebbing vitality*)." The requisite evidence is afforded in the experience of gardeners who generally consider spiny plants as "always given to die back," or as otherwise expressed, they "often prune themselves." It is difficult to adduce the same kind of evidence among animals, though there may be some degree of semblance between this self-pruning of spiniferous plants and the growth, death, and shedding of the antlers of the modern Deer. Stronger evidence of the relations of spinosity to the organism is afforded in the consideration of spines as consisting wholly of the mechanical tissues. They are more or less dead structures and are usually without special physiological function. Hence, in so far as the whole or a part of an organism is spinose, it represents the ratio between the mechanical and active tissues, or between the inert and living structures.

Morris[40] correlates the mechanical and motor defenses of animals and plants in a matter bearing upon this subject as follows: "If we examine the whole range of the animal kingdom, we find every phase of combination of mechanical and motor defense, the motion growing more sluggish as the defensive armor grows more efficient. But in the whole kingdom, motion persists as one of the defensive agencies. No animal exists without some power of motion, by whose aid it withdraws or otherwise escapes from danger." He also notes that the plant kingdom, with the exception of the minute, swimming forms, possesses no defensive motion, and that mechanical defense alone exists. Under mechanical defense are included thorns, spines, etc., together with chemical appliances, as in plants with poisonous or disagreeable juices. These facts lead to the conclusion that, in proportion as animals are spinose or armored, they exhibit a vegetative type of structure, and have retrograded.

It has been shown elsewhere in this article, that the greatest development of spinose organisms occurs just after the culmination of a group, and, as this period clearly represents the beginning of the decline of the vitality of the group, the spines are to be taken as the visible evidence of this decadence. A similar observation has been made by Packard,[44] who after passing in review the geological development of the Trilobites, Brachiopods, and Ammonites, states that "these types, as is well known, had their period of rise, culmination, and decline, or extinction, and the more spiny, highly ornamented, abnormal, bizarre forms appeared at or about the time when the vitality of the type was apparently declining."

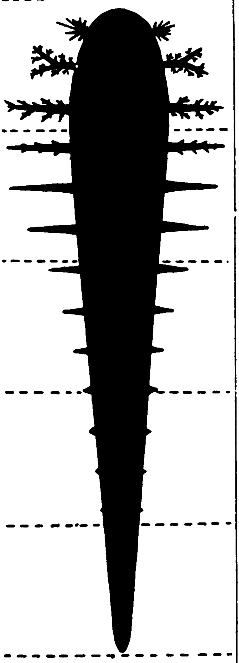
Furthermore, it is now commonly agreed that all groups have been most plastic near their point of origin, or, in other words, that during their early history, all the important or major types of structure have been developed. Their subsequent history reveals the amount of minor differentiation and specialization they have undergone. Apparently, most of the early impulses of growth, whether from the environment or from vital forces, resulted in physiological changes producing fundamental variations in function and structure. The later influences of environment and growth force are expressed in peripheral differentiation, and show that the racial or earlier characters had become fixed, and that the later or specific features were the chief variables. The stimuli which, during the early life history of a group, were expended in internal or physiological adjustments, later produce external differentiation, and in this differentiation, spinosity is the limit. The presence of spines, therefore, indicates the fixity of the primary physiological characters, together with the consequent inability of the organism to change due to its decreasing vitality.

Conclusion.

Just as all our features of terrestrial topography are included between the limits of plains and mountains, and the mountains are considered as the limit of progressive accidentation, so the spines of animals or the monticules and pinnacles of their surface may be considered as the limits of progressive differentiation. The primitive base level, or peneplain, becomes elevated, and by erosion is cut up into table lands, mèsas, and buttes, with intersecting valleys. The valleys are gradually deepened, and the country becomes rougher until a maximum is reached. Then follows a reduction of the inequalities of the surface, and finally in old age, the smooth, gently rounded outlines of geographic infancy again appear. So in organisms, the smooth rounded embryo or larval form progressively acquires more and more pronounced and highly differentiated characters through youth and maturity. In old age, it blossoms out with a galaxy of spines, and with further decadence produces extravagant vagaries of spines, but in extreme senility comes the second childhood, with its simple growth and the last feeble infantile exhibit of vital power.

The history of a group of animals is the same. The first species are small and unornamented. They increase in size, complexity, and diversity, until the culmination, when most of the spinose forms begin to appear. During the decline, extravagant types are apt to develop, and if the end is not then reached, the group is continued in the small and unspecialized species, which did not partake of the general tendency to spinous growth.

Lastly, it must be determined whether spines are really hereditable characters, and therefore can be used in studying the phylogenies of groups. No one has yet been able to show any type or set of characters which cannot be transmitted from parent to offspring. Hyatt[34] says: "Everything is inherited or inheritable, so far as can be judged by the behavior of characteristics." Furthermore, in a review of animal life, extinct and living, no one can fail to be impressed with the fact that, especially near the close of the life history of a group, or in a series of highly specialized forms, spinose characters are often considered as of supra-varietal value, and are rated of specific, generic, and sometimes of family rank, or even higher. They have therefore acquired a fixed importance in these special groups, and are recognized in the same categories with physiological and structural characters. The differences which appear at an early period in higher genera are the bases of distinction among lower genera. If the spines or other similar features do not make their appearance in an individual until a late adolescent stage, they are usually of negative value in a scheme of classification. This agrees with the general principle recently suggested by Harris,[32] that when the main features of the ornament (= spines, etc.) are foreshadowed in the larval and early adolescent stages, they are to be regarded as of taxonomic value.



Ontogeny stages.	Ontogeny condition.	Phylogeny stages.	Phylogeny condition.	Chronology.
Old age or gerontic	Paraplasis	Phylogerontic	Paracme	5
Adult or ephebic	Metaplasis	Phylephebic	Acme	4
Immature or neanic	Anaplasis	Phyloneanic	Epacme	3
Larval or nepionic	Anaplasis	Phylonepionic	Epacme	2
Embryonic	Anaplasis	Phylembryonic	Epacme	1

Diagram and table showing correlation of stages and conditions of development in the spinose individual, in its ancestry, and in time.

The preceding diagram illustrates the previous statements, and shows the correlation between the stages and conditions of growth in the ontogeny of a spinose individual, with its phylogeny, and also the chronology of groups containing spinose forms. The numbers indicating chronology simply refer to successive periods of time. In particular cases, they may be long geologic ages as Cambrian, Ordovician, Silurian, Devonian, and Carboniferous, or in other instances they may represent much shorter periods.

From the study of the ontogenies of spinose forms, it has already been ascertained that they were simple and inornate during their young stages; and from the phylogenies of the same and similar forms, it was likewise learned that they were all derived from non-spinose ancestors. It has also been shown that spines represent an extreme of superficial differentiation which may become fixed in ontogeny, and the further conclusion, that spinosity represents a limit to morphological and physiological variation, has been reached. Finally, it is evident that, after attaining the limit of spine differentiation, spinose organisms leave no descendants, and also that out of spinose types no new types are developed.

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